THE ECOLOGY OF SMELT, *Osmerus eperlanus* (Linnaeus), FROM THE RIVER THAMES AND THE RIVER CREE.

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ABSTRACT

This thesis presents ecological data for the smelt, (Osmerus eperlanus (L)), a species which has hitherto been almost totally excluded from ichthyological investigations in Britain. Samples were obtained from the river Thames on a monthly basis between February 1981-May 1982, and from the river Cree during the spawning migrations in March 1980 and 1981 and on a seasonal basis between autumn 1981 and summer 1982.

The past and present commercial value of smelt stocks has been compared and the present distribution of the species in Britain mapped. Limitations in the legislative protection afforded to smelt have been identified and the possibilities for re-introduction by means of artificial propagation discussed.

Smelt scales were found to provide a rapid method of age determination but length was found to be a poor predictor of age. Smelt from both study sites exhibited short-cycle life histories with no fish having formed a fourth annulus. There were marked changes in sex ratio with age indicating a sex selective mortality which the literature has attributed to a higher post spawning mortality of male smelt. Growth after the fall occurred at both study sites and in the river Thames the main growth period occurred between June-December. A hypothetical birth date of 1st June was assumed. Smelt from both study sites exhibited the greatest instantaneous growth in length in the first year of life, a pattern of growth typical in temperate smelt populations. The growth rate of Cree smelt ($L\infty$ = 283 mm) was much greater than that in the Thames ($L\infty$ = 187 mm) possible reasons for which have been discussed. Female smelt were generally larger than males of an equivalent age although the differences were rarely

significant. Seasonal variation in condition was followed and at both sites the peak total condition corresponded with the peak in the cycle of gonad development. The development of gonads did not appear to be at the expense of somatic condition.

The seasonal pattern of gonad development was followed for smelt from both study sites and the investment in reproduction compared between sexes and between study sites. Peak gonad development occurred earlier in male smelt than in females. Insignificant differences occurred in the mean gonadosomatic ratio of Thames and Cree males but female Cree smelt had significantly higher gonadosomatic ratios than female Thames smelt of the same age. Absolute fecundity, relative fecundity and egg diameters were studied at both sites and predictive equations for fecundity were derived from multiple regression analysis. Thames smelt were characterised by higher relative fecundity but smaller egg size than Cree smelt. Within a given study site no clear relationship between egg size and fish size was evident. 21 (2.6%) Thames smelt were identified as being synchronous hermaphrodites and these individuals were compared with other hermaphroditic smelt. Smelt from the river Cree first matured at approximately 2 years of age as reported from many other populations. In the Thames however, the 1981 year class contained mature 0-group specimens presumably as a result of improved first year growth. The population dynamics of spawning smelt were monitored from the migrations into the river Cree in 1980 and 1981. The run was characterised by marked changes in size, age and sex ratio and possible factors involved in initiating the spawning migration were discussed.

The diet of smelt was found to comprise 4 major food categories - Mysidae, Gammaridae, Crangonidae and various species of

young fish, and cannibalism was present in the river Cree. The diets from both study sites were significantly correlated although mysids and gammarids dominated in the diet of Thames smelt and Crangon crangon and young fish, particularly underyearling smelt, dominated in the diet of Cree smelt. Seasonal variations in the composition of the diet were marked particularly in the case of Thames smelt where mysids and gammarids exhibited alternating peaks of dominance in the diet. Possible reasons for both seasonal variations in the diet and variations in the diet with age (size) have been discussed. A new non-subjective index of feeding activity, here termed the volumetric index, has been devised. 0-group fish were found to feed more intensively than older fish.

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CHAPTER 1: INTRODUCTION

Smelt, of the family Osmeridae, are small salmonoid fishes inhabiting the temperate and arctic waters of the northern hemisphere. The family includes two subfamilies - the Osmerinae (comprising the genera Osmerus, Spirinchus, Thaleichthys and Allosmerus) and the Hypomesinae (comprising the genera Hypomesus and Mallotus) (McAllister, 1963).

Three forms of the boreal smelt, *Osmerus spp*., have generally been recognised. These are:-

(i) *Osmerus eperlanus* (Linnaeus) of north-western Europe

(ii) *Osmerus dentex* Steindachner of the north Pacific and arctic waters of both north-western North America and Asia

(iii) *Osmerus mordax* (Mitchill) of north-eastern North America.

This trispecific designation had been questioned since the turn of the century (eg. Berg, 1909; Hubbs, 1925) but it was not until 1963 that the views of these early systematists were given scientific support. In that year, a thorough review of the family Osmeridae (McAllister, 1963) provided evidence that the genus Osmerus contained only one species, *Osmerus eperlanus* with two subspecies, *Osmerus eperlanus eperlanus* and *Osmerus eperlanus mordax*. In contrast, Kluikanov (1969) considered that the genus should include *Osmerus eperlanus* as a full species and *Osmerus mordax mordax* and *Osmerus mordax dentex* as subspecies. McPhail and Lindsey's (1970) study of smelt throughout North America added to the taxonomic confusion and they concluded by adopting the term '*Osmerus eperlanus* complex' with the common designation 'boreal smelt'. Whilst this would appear to be a realistic attitude in view of the systematic confusion, Scott and Crossman (1973) considered that such a grouping would prevent clarity of thought and the exchange of information.

Recent work by McAllister (1980, manuscript) has resulted in a further revision of the genus such that two forms of the European smelt have now been identified. In addition, some of the forms described by Rembiszewski (1970) may also require recognition as distinct species or subspecies.

Until the taxonomic confusion surrounding the smelt, a polytypic species with many geographical and ecological forms (Belyanina, 1969), has been clarified, the trispecific system would appear to be the most acceptable for ease of discussion. With the exception of taxonomic studies, this system is still widely adopted in the current literature. The present multivariate taxonomic study of the European smelt (McAllister, personal communication) will undoubtedly help to clarify the systematics of the genus, but until the results of this study are available the most acceptable system would appear to be the trispecific division.

Samuels (1904) described smelt as "one of the neatest, most graceful and delicate of all our food fishes". They are characterised by a fusiform, laterally compressed and elongate body with the maximum body depth occurring anterior to the dorsal fin origin. The head is pointed and of moderate length with eyes of moderate size and a nearly flat inter-orbital region (Regan, 1911). The large mouth is terminal and oblique with the mandible curved upwards and protruding and the maxillae extending behind the posterior edge of the orbit (Day, 1884; Scott and Crossman, 1973). Dentition is well developed in the genus Osmerus with teeth being present on the vomer, palatine, pterygoid, basibranchial, dentary, maxillary, premaxillary and tongue, with large canine teeth on the vomer and tongue (McPhail and Lindsey, 1970; Scott and Crossman, 1973). The specific names mordax (biting) and dentex (toothed) reflect the ferocity of the dentition. In November 1966 several match anglers on the river Trent at Littleborough caught smelt which, on the basis of their dentition, were identified as the dreaded (in certain angling circles) zander, Stizostedion lucioperca. The true identity of the fish was later revealed, much to the relief of the anglers and Trent Water Authority official alike (Cacutt, 1979).

Regan (1911) regarded the external characteristics of the smelt, particularly the presence of an adipose fin, to be typical of the salmon family. Bigelow and Schroeder (1953) considered that the combination of a slender form, a pointed head, an adipose fin and a deeply forked caudal fin was sufficient to distinguish the smelt, Osmerus mordax, from all other fish common in the Gulf of Maine. MacMahon (1946) believed that the same characters prevented confusion of the smelt, Osmerus eperlanus, with any other British fish. However, the common designation smelt has also been applied to the unrelated sand smelt, Atherina presbyter, which has caused some spurious data regarding the distribution of Osmerus eperlanus in Britain (see Chapter 3).

Superiorly, the smelt or sparling is light olive green in colour, becoming silver below with purple, blue and pink irridescent reflections when freshly caught (Day, 1884; Scott and Crossman, 1973). Juvenile smelt do not possess such vivid colouration and appear transparent when initially removed from the water. Johnson (1884) suggested that this transparency was responsible for the name smelt since the fish appeared to be melting away as would materials undergoing smelting! Regan (1911) dismissed this explanation and stated that the name was undoubtedly derived from the anglo-saxon word smeolt, meaning smooth and shining.

Probably the most distinguishing characteristic of the smelt is its smell which has been variously compared to cucumbers, violets and freshly cut rushes (Day, 1884) and which has resulted in the fish being known colloquially as the 'cucumber fish'. The German colloquiallism 'stinkfish' is an epithet which Linnaeus considered to be entirely warranted. Scott and Crossman (1973) believed the smell was responsible for the name smelt, or literally 'smell it' and support for this argument comes from the generic name Osmerus which is derived from the Greek word osme meaning scent or smell.

The odouriferous substance is localised in the skin, although not all people are capable of detecting it (Bigelow and Schroeder, 1953). Several other species of fish possess these odouriferous substances, the most well known being the grayling, Thymallus thymallus. Complex analysis using computer linked gas chromatography-mass spectrophotometer systems has identified trans-2-cis-6-nonadienal, a major constituent of cucumbers, as the odouriferous substance present in Australian grayling, Prototroctes maraena (Berra, Smith and Morrison, 1982). An isomer of this substance, 2, 4-dimethyl-2, 4 heptadienal, has been identified in Osmerus mordax (Geiselman, 1972). The role of these chemicals in the biology of the smelt is purely conjectural but they may be alarm substances. Day (1884), Southwell (1887a) and Belyanina (1969) believed that the smell drove away other fishes, "thus protecting the smelt from its enemies" (Day, 1884). In the case of the Australian grayling the substance may be a by-product of a partly vegetarian diet since several algae are known to emit a cucumber odour (Berra et al, 1982). In the case of the carnivorous smelt, bioaccumulation of these substances through the food chain would have to be demonstrated.

The smelt is a gregarious and voracious (Day, 1884) pelagic species (Scott and Crossman, 1973), which inhabits the estuaries and lower reaches of unpolluted rivers (Maitland, 1974). In the early spring smelt assemble in shoals and ascend the rivers to spawn. While spawning usually takes place at the head of the tide, in some populations a proportion of the fish may migrate well beyond the zone of tidal influence (Regan, 1911; Leim and Scott, 1966). Since the smelt is an inshore species, the spawning migrations are usually over relatively short distances (< 20 km) although in the Yenisey river spawning fish may travel distances of up to 1000 km (Kuznetsova, 1962) (in Belyanina, 1969).

The dominant and most successful way of life appears to be an anadromous, estuarine existence although the smelt can complete its entire life-cycle in freshwater (Scott and Crossman, 1973) as evidenced by their introduction and phenomenal spread throughout the Great Lakes (Van Oosten, 1937). Day (1884) stated that a Colonel Meynell, of Yalm in Yorkshire, kept smelt for four years in a freshwater pond, and Southwell (1887a) made reference to smelt being kept alive in freshwater tanks prior to their sale at Norwich fish market. The only breeding landlocked population of smelt in Britain occurred at Rostherne Mere, Cheshire but the population died out in the 1920's (Maitland, 1979) probably as a result of eutrophication

(Maitland, personal communication). The smelt is incapable, however, of establishing populations in the lotic environment and only enters streams at spawning time (Scott and Crossman, 1973).

The smelt, Osmerus spp., has been renowned as a food fish for decades and it supports fisheries in many places including the Great Lakes and the arctic rivers of the USSR, and at one time was the staple diet of the natives in the Bristol Bay area (McPhail and Lindsey, 1970). In 1966, the global yield of Osmerus was 28 x 10^3 metric tons, of which 16.6 x 10^3 tonnes was landed in Russian waters and 3.5 x 10^3 tonnes on the North American continent (FAO, 1966). The majority of this commercial catch was derived from the lacustrine rather than the estuarine environment. Thus, in 1960 the Great Lakes yielded 7264 tonnes (Bailey, 1964) and between 1931-63 Pskovsko-Chudskoye lake yielded an average of 3600 tonnes per annum. In contrast, the river Miramichi fishery in New Brunswick yielded an average of 726 tonnes per annum between 1931-63 (McKenzie, 1964) and the drainages of the White Sea yield 400 tonnes per annum (Belyanina, 1969).

In Newfoundland, Quebec and parts of the Maritime Provinces, the smelt, Osmerus mordax, is also an extremely popular sport fish, being taken by means of dipnetting and seining during the spawning runs and by winter angling through the ice (Scott and Crossman, 1973). In Ontario, spring smelting expeditions are extremely popular and over a two week period in 1959 a total of 62000 sport fishermen harvested around 1500 tonnes of smelt from Lake Erie alone (Roseborough, 1960). Rostlund (1952) attributed the great value of smelt to the fact that they are in best condition and most abundant in winter when other fishes are scarce or hard to catch.

Izaak Walton (in Cacutt, 1979) spoke of 2000 people fishing for smelt between London Bridge and Greenwich on the Thames and MacMahon (1946) considered it unfortunate for London anglers that pollution and over fishing resulted in the loss of "such a sporting and tasty quarry". Today, the smelt in Britain has little or no recreational value although the annual spawning migration into the river Cree creates much interest amongst local townsfolk and a small number of people prefer to 'angle their bucketful'. Elsewhere in Britain the appearance of smelt in the catch of anglers tends to cause much bewilderment as evidenced by recent reports in the angling press (eg. Anglers Mail, 1980).

The presence of a large number of spawning fish in a river system also creates considerable interest amongst wildlife enthusiasts. The aesthetic aspects of the runs of alewives, Alosa pseudoharengus, into the rivers of Cape Cod have been dealt with by Hay (1959).

The smelt, Osmerus spp., is also of considerable importance as a forage base, and is preyed upon by many species of fish including cod, Gadus morhua, (Belyanina, 1969); pike, Esox lucius (Coward, 1912b; Belyanina, 1969); perch, Perca flavescens and Perca fluviatilis (Kendall, 1927; Schneberger, 1936; Belyanina, 1969); lake trout, Cristivomer namaycush; burbot, Lota lota (Kendall, 1927; Schneberger, 1936) brook trout, Salvelinus fontinalis; eel, Anguilla rostrata; walleye, Stizostedion vitreum; bass, Micropterus dolomieu (Kendall, 1927); ide, Idus idus (Cala, 1970); four-horned sculpin, Myxocephalus quadricornis (Westin, 1970); and pike-perch, Stizostedion lucioperca (Belyanina, 1969). Willemson (1977) showed that smelt was the preferred food of pike-perch in Holland.

The value of smelt as a forage species reaches its peak in the management of the economically valuable salmonids. The importance of smelt, Osmerus mordax, as a forage base for landlocked Atlantic salmon, Salmo salar, is considerable and has been documented by Rupp (1959, 1968), Havey and Warner (1970), Warner (1972) and Havey (1973). The latter named study showed that the establishment of smelt as forage markedly increased the growth of the salmon population resulting in a highly satisfactory fish for sport fishing purposes. Havey (1973) concluded that in any contemplated introduction of salmon to lakes, smelt or a substitute forage if not already present should be routinely introduced with the salmon.

Ney (1981), considered some of the attributes of an ideal forage species and concluded that the species should be prolific, stable in abundance, trophically efficient, vulnerable to predation, non-emigrating and innocuous to other species. While the smelt satisfies most of these criteria, it suffers from considerable fluctuations in abundance (Rupp, 1968). One of the most catastrophic natural mortalities ever recorded for a North American animal involved the smelt, Osmerus mordax, populations of Lakes Huron and Michigan. First signs of the die-off, widely believed to be of viral origin, occurred in the autumn of 1942 and the total loss from 1942 to 1946 was estimated at 25000 tonnes. The mortality all but wiped out the population (Van Oosten, 1944).

Furthermore, considerable conflict has arisen as a result of the possible effect of smelt introductions on the native fish fauna at the same or lower trophic levels.

In Britain no quantitative investigation of the forage value of smelt, Osmerus eperlanus, has been undertaken although Falkus (1975) presents evidence that suggests that smelt may be a locally important food of sea-trout, Salmo trutta, and Menzies (1936) found that sea-trout kelts in the Firth of Forth gorged themselves on smelt upon returning to the estuary. The annual report of the Inland Fisheries Trust of Ireland (1970) also believed that smelt shoals must attract large slob trout and bass but concluded that more needed to be known regarding the extent to which they serve as forage for predatory species.

The value of smelt resources in Britain is currently regarded as being of scientific (commercial) value only (Maitland, 1974). Large fisheries once existed for this species in the Firth of Forth, Solway Firth (Day, 1884; HMSO, 1892), Norfolk waters (Southwell, 1887a), the Thames (Regan, 1911) and to a less well documented extent throughout its British range. However, by the turn of the century over fishing and/or pollution of the rivers had resulted in a severe reduction in the commercial smelt fisheries (Masterman, 1913). At this time, the need for regulating the fishery was appreciated:

> "under proper regulations we believe that sparling fishing might be restored to its position as one of the more valuable fishing industries of the Solway. At present it has suffered deterioration owing to indiscriminate capture and the absence of a close-time, and unless steps are taken to preserve the fish they will soon become a thing of the past" (HMSO, 1892).

In British waters the smelt has also suffered from a lack of scientific investigation. Although an extensive bibliography is available for the family Osmeridae on a global scale (Gruchy and McAllister, 1972), information regarding the smelt in Britain is scant. Early texts on British freshwater fishes eg. Yarrell (1836), Day (1884), Buckland (1891) and Regan (1911) gave descriptions of the smelt, its fisheries and habits, but provided no quantitative data. Despite the statement by Buckland (1891) that "among the Salmonidae the smelt, or sparling, requires more attention than he has hitherto received", it was not until 1913 that Masterman (1913) published the results of an eight month study of the morphology of smelt scales and their validity in age determinations. However, the use of pooled averages imposed severe limitations on the conclusions that could be drawn from this publication regarding growth rate and condition.

The landlocked population of smelt in Rostherne Mere, Cheshire, afforded a unique opportunity to study smelt in the freshwater environment. Smelt were known to have been inhabitants of the Mere from the early eighteenth century but they were totally ignored by ichthyologists. Even reports signalling a possible decline in the population (Coward, 1912a, 1912b, 1916, 1924) failed to stimulate scientific investigation and the population became extinct before any contribution to the biology of the species could be made.

With the exception of Maitland's (1972) distribution map and several estuarine studies that have included small quantities of data regarding smelt (Huddart, 1971; Van den Broek, 1977; Sedgwick, 1979) no biological studies of smelt have been carried out in Britain since Masterman (1913). As recently as 1970, the state of our knowledge of smelt was summarised in the annual report of the Inland Fisheries Trust of Ireland (1970) which concluded that "more needs to be known about their [smelt] distribution and habits".

The objective of this thesis is to provide baseline ecological data which could be used as the rationale for management or preservation of the smelt in the future. It is hoped that the information contained herein will stimulate interest in, and provide pointers for future research on, a species which has hitherto been scientifically ignored by British ichthyologists.

CHAPTER 2: GENERAL METHODOLOGY

2:1 SAMPLING SITES

Smelt were obtained from the river Thames, England, on a monthly basis between February 1981 and May 1982, and from the river Cree, Scotland, during the spawning runs in March 1980 and 1981, and on a seasonal basis between November 1981 and July 1982.

2:1:1 River Thames

The causes, extent and amelioration of the gross organic pollution of the Thames, England's longest river, have been documented by HMSO (1964), Potter (1971) and Wheeler (1979).

Until the early 1960's anaerobic conditions existed in some part of the river throughout the year, and depending on the physical conditions, particularly flow rate and temperature, up to 32 km of the river may have been anaerobic. The subsequent rehabilitation of the Thames estuary has received considerable attention in the scientific literature (eg. Wheeler, 1968a, 1968b, 1969a, 1971, 1979; Huddart, 1971; Huddart and Arthur, 1971a, 1971b; Solomon, 1975; Elkington, 1977; Sedgwick, 1979; Andrews, 1977; Andrews and Rickard, 1980; Andrews, Aston, Rickard and Steel, 1982) and has culminated in the return of the salmon, Salmo salar, (Solomon, 1975; Anon, 1982; Higgins, 1982). The recolonisation of the Thames tideway by the smelt will be dealt with in Chapter 3.

Monitoring the return of fish to the Thames estuary has been facilitated by the presence of several power stations (eg. CEGB Fulham, Brunswick Wharf, Blackwall Point, Barking, Littlebrook, West Thurrock and Tilbury) which abstract cooling water from the Thames. Although the initial monitoring at these power stations was purely qualitative

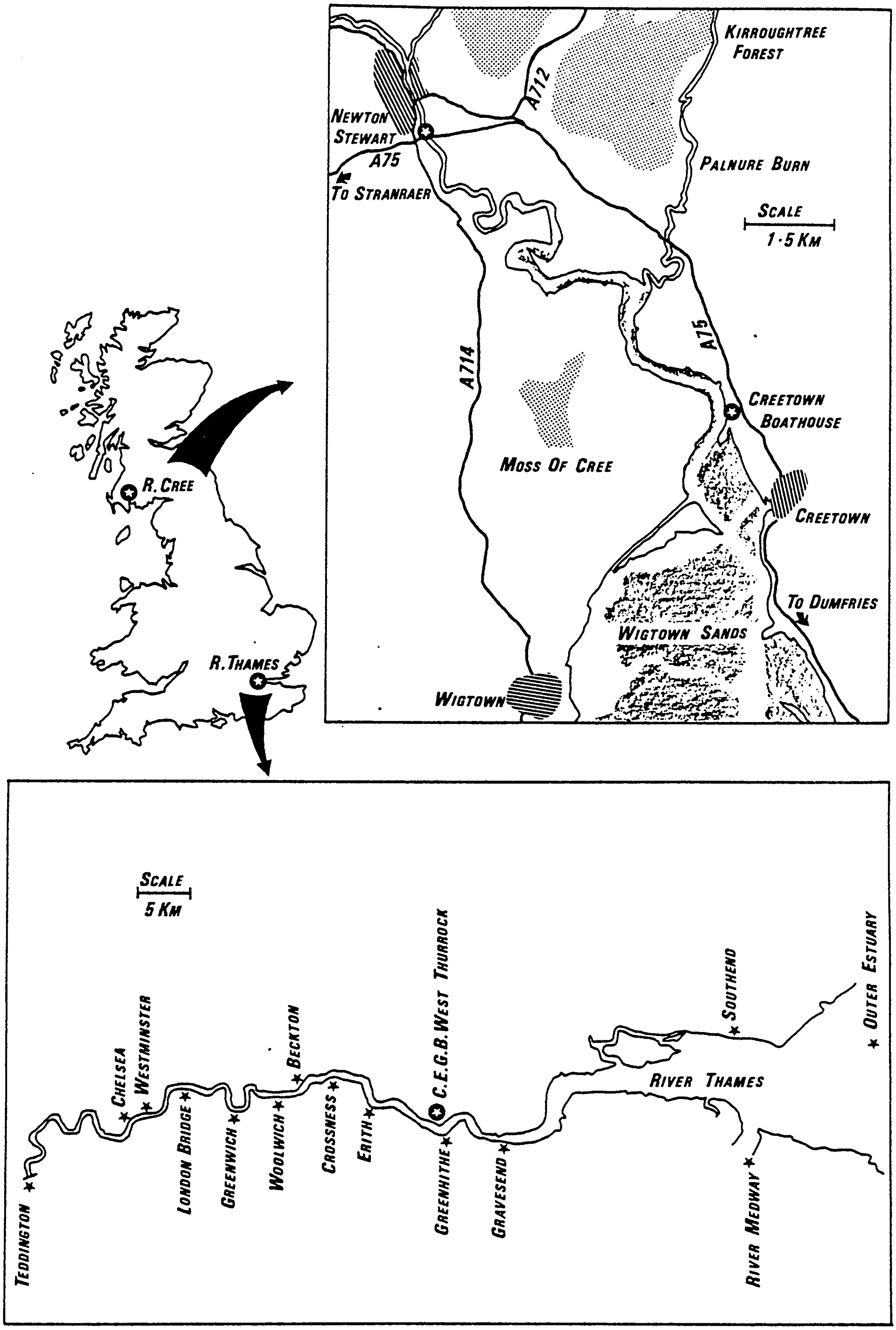


FIGURE 1: Location of the sampling sites (✪).

in nature eg. Wheeler (1968b), the procedure devised by Huddart (1971) enabled power station screening apparatus to be used as a quantitative nekton sampler. The composition, relative abundance and temporal distribution of the nekton in the middle Thames estuary could therefore be determined. A modification of Huddart's (1971) procedure, which relates catches to the volume of throughput water (0.45×10^6 m^3 per sampling period) has been incorporated into a routine sampling programme by the Metropolitan Pollution Control Division of Thames Water Authority at one of the power stations, CEGB West Thurrock. The smelt samples analysed in this work were all obtained from screen catches at CEGB West Thurrock. The dates of sampling and the numbers of smelt in each sample are shown in Table 1.

The classical system of locating points along the Thames estuary relates any site upstream (+) or downstream (-) to the position of London Bridge. Estuarine conditions are delimited by Teddington Weir (+ 29.5 km) at the upstream extremity and, while the seaward extension of the estuary is indistinct, salinity levels approach marine conditions seaward of Southend (- 70 km) (Sedgwick, 1979). CEGB West Thurrock is located (-) 35.5 km downstream of London Bridge.

Andrews et al (1982) divided the estuary into eight zones according to their respective half-tide salinities, ranging from zone 1 (1-2°/₀₀) above London Bridge to zone 8 (35°/₀₀) in the outer estuary. CEGB West Thurrock is located in zone 4, and is characterised by half-tide salinities in the range 11 - 17°/₀₀. The composition of the catch at CEGB West Thurrock reflects the salinity range and is dominated by euryhaline and marine species. However, freshwater fish

MONTH	DATE OF SAMPLING	DAY NO. FROM 1st JANUARY	NO. OF DAYS BETWEEN SAMPLES	NO. IN SAMPLE (n)
FEBRUARY	9. 2.81	40		51
MARCH	2. 3.81	61	21	56
APRIL	7. 4.81	97	36	77
MAY	**	**	**	**
JUNE	4. 6.81	155	**	38
JULY	2. 7.81	183	28	38
AUGUST	18. 8.81	230	47	64
SEPTEMBER	16. 9.81	259	29	39
OCTOBER	2.10.81	275	16	60
NOVEMBER	2.11.81	306	31	70
DECEMBER	15.12.81	349	43	70
JANUARY	28. 1.82	28	44	56
FEBRUARY	26. 2.82	57	29	38
MARCH	12. 3.82	71	14	60
APRIL	26. 4.82	116	45	60
MAY	25. 5.82	145	29	40
				817

TABLE 1: Dates of sampling and the number of smelt collected on a monthly basis from the cooling water screens at CEGB West Thurrock.

SPECIES	NUMBER CAUGHT	
Whiting, Merlangius merlangus (L)	54944	(6439)
Sand goby, Pomatoschistus minutus (Pallas)	47928	(2978)
Flounder, Platichthys flesus (L)	44540	(4648)
Smelt, Osmerus eperlanus (L)	35657	(2484)
Herring, Clupea harengus (L)	34370	(3719)
Sprat, Sprattus sprattus (L)	17424	(3005)
Sole, Solea solea (L)	7153	(353)
Pouting, Trisopterus luscus (L)	4916	(822)
Bass, Dicentrarchus labrax (L)	1871	(262)
Eel, Anguilla anguilla (L)	1836	(91)
Dab, Limanda limanda (L)	1543	(210)
Poor cod, Trisopterus minutus (L)	1469	(100)
Nilsson's pipefish, Syngnathus rostellatus Nilsson	1293	(213)
Common sea snail, Liparis liparis (L)	1019	(181)
Three-spined stickleback, Gasterosteus aculeatus (L)	999	(69)
Hooknose, Agonus cataphractus (L)	918	(179)

TABLE 2: The dominant species of fish in the screen catches at CEGB West Thurrock. The numbers refer to the total number collected during 1975-1981 with peak catches per sampling period in parentheses. (Modified from Andrews et al, 1982)

MONTH	SUSPENDED SOLIDS (mg/l)	CONDUCTIVITY μ_s/cm	pH	DISSOLVED OXYGEN % Saturation	DISSOLVED OXYGEN mg/l	BOD*	NITROGEN (mg/l) NH_4	NITROGEN (mg/l) TON	SALINITY °/°°
JANUARY	111.5	20750	7.4	73.6	8.1	1.9	0.22	-	13.7
FEBRUARY	115.5	22666	7.1	67.0	7.3	1.6	0.17	7.7	16.7
MARCH	102.2	18600	7.2	67.3	7.2	1.7	0.28	8.2	11.4
APRIL	88.5	-	7.3	58.4	5.9	1.4	0.10	8.1	10.0
MAY	104.0	-	7.3	53.2	5.2	2.0	0.10	6.9	12.1
JUNE	57.8	-	7.3	52.3	4.7	1.6	0.04	6.4	12.8
JULY	49.3	-	7.5	54.0	4.6	1.0	0.09	6.1	17.6
AUGUST	44.3	28500	7.1	48.6	4.0	1.6	0.04	5.7	17.8
SEPTEMBER	76.0	30500	7.2	52.4	4.4	1.3	0.05	5.7	18.9
OCTOBER	105.3	22500	7.2	58.2	5.5	1.1	0.10	6.9	15.8
NOVEMBER	98.6	22600	7.3	60.7	6.1	1.2	0.12	7.1	14.7
DECEMBER	158.0	20000	7.6	71.2	8.0	3.3	0.67	5.6	12.6
JANUARY	61.7	10233	7.3	75.1	9.0	2.3	0.86	8.1	7.1
FEBRUARY	73.2	16649	7.4	69.8	7.7	1.9	0.67	7.2	10.1
MARCH	69.4	18070	7.4	66.7	7.2	1.5	0.26	7.7	10.6
APRIL	99.3	19432	7.5	60.1	6.1	1.5	0.09	7.3	12.7
MAY	84.0	23875	7.6	62.7	5.9	1.7	0.07	6.8	15.7

* Oxygen consumed in five days at 20°C

TABLE 3: Water quality parameters for the river Thames off CEGB West Thurrock (Greenhithe). Values are monthly means derived from weekly samples.

species such as carp, Cyprinus carpio, bream, Abramis brama, and roach, Rutilus rutilus, occur sporadically particularly during periods of high freshwater flow. To date, 76 species of fish have been recorded from the screens at CEGB West Thurrock (Andrews et al, 1982) and those species occurring most frequently in Thames Water Authority samples between 1975 and 1981 are shown in Table 2.

Water samples and temperature data were collected on a weekly basis off Greenhithe (see Figure 1) by Thames Water Authority staff aboard sludge boats. Monthly averages of various water quality parameters are presented in Table 3, and air and water temperatures are shown in graphical form in Figure 2. Conditions in the estuary are extremely turbulent and vertical mixing is therefore extensive. The physico-chemical gradients can therefore be considered to be unidirectional along the length of the estuary (Sedgwick, 1979).

Andrews et al (1982) drew attention to the fact that the recovery of the macroinvertebrate fauna had been poorly documented compared to the literature regarding the fish populations. These authors go a long way towards remedying this situation by presenting a comprehensive, qualitative list of invertebrates covering the whole of the estuary. Unfortunately, however, quantitative samples necessary for estimating the degree of prey selection by smelt are not available.

2:1:2 River Cree

The river Cree drains an area of approximately 368 km^2, the geology of which consists of Silurian greywackes and shales of the Llandovery-Taranon and Llandeilo-Caradoc series. Agricultural development, with the exception of forestry, is severely restricted

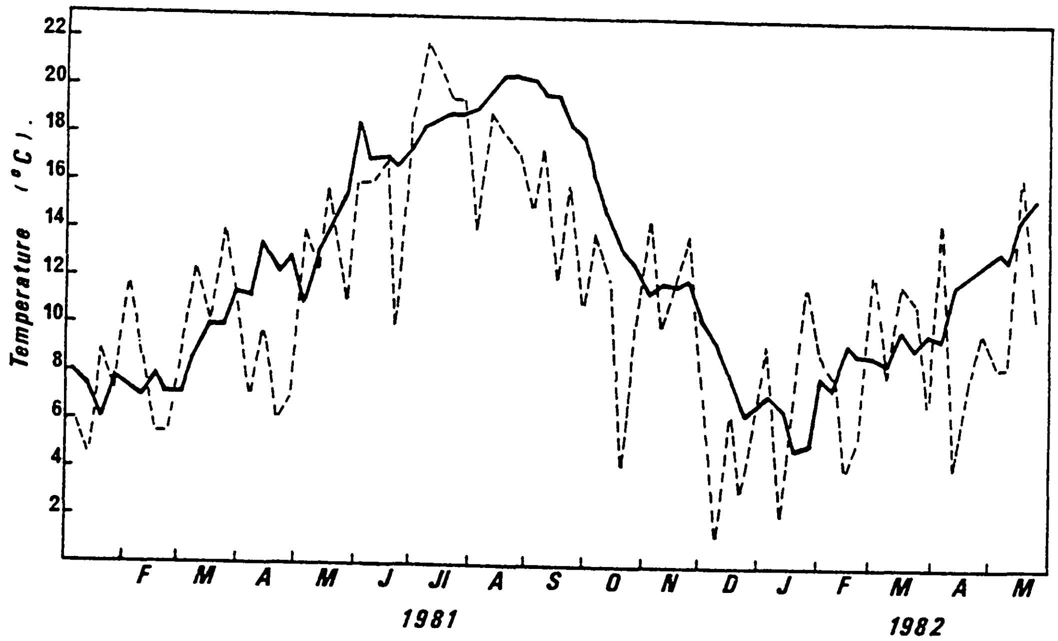


FIGURE 2: The seasonal pattern of water (———) and air (-----) temperatures at Greenhithe on the river Thames based on weekly measurements.

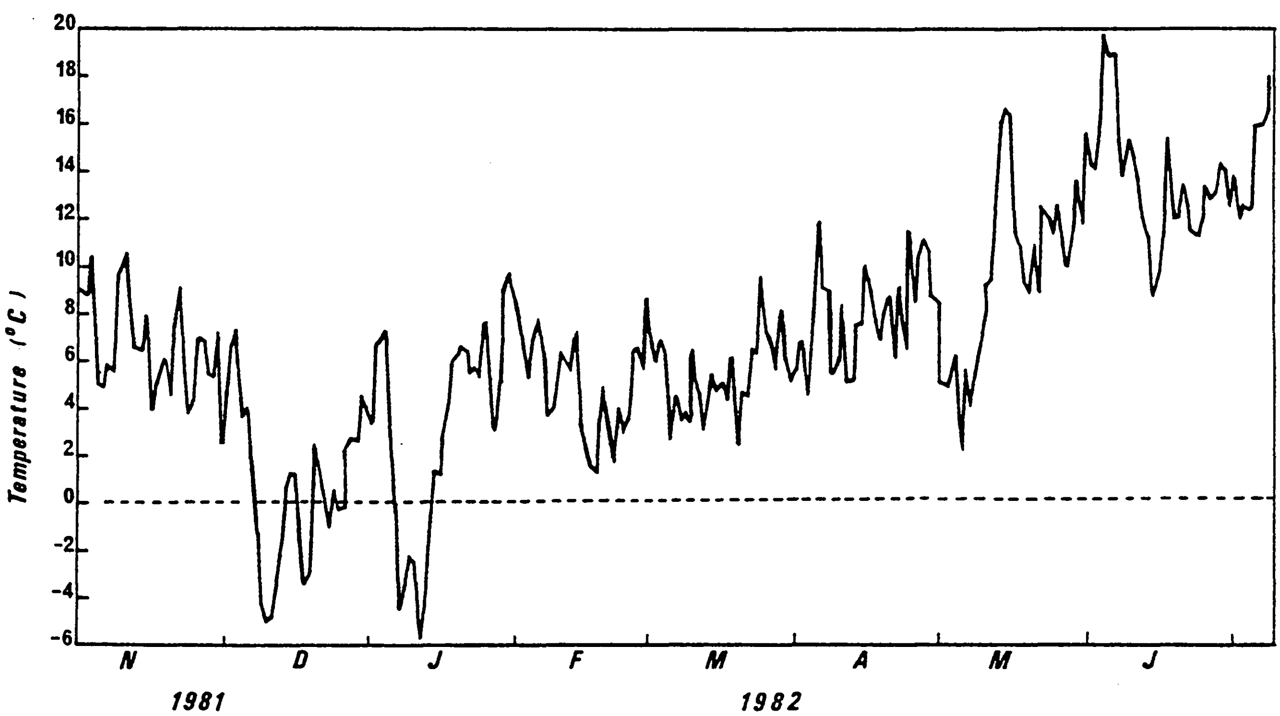


FIGURE 3: The seasonal pattern of mean daily air temperatures for the Cree estuary.

SEASON	DATE OF SAMPLING	DAY NO. FROM 1st JANUARY	NO. OF DAYS BETWEEN SAMPLES	NO. IN SAMPLE (n)
SPRING SPAWNING RUN	10. 3.80 - 16.3.80	70 - 76	-	278
SPRING SPAWNING RUN	10. 3.81 - 14.3.81	69 - 73	-	236
AUTUMN	2.11.81	306		64
			108	
WINTER	18. 2.82	49		57
			58	
SPRING	17. 4.82	107		86
			78	
SUMMER	4. 7.82	185		47
				768

TABLE 4: Dates of sampling and the numbers of smelt collected from the river Cree

WATER QUALITY PARAMETER (mg/l unless stated)	MEAN VALUE (min - max)
SUSPENDED SOLIDS	165 (34 - 296)
pH (pH units)	7.1 (6.1 - 7.8)
BOD *	1.8 (0.2 - 2.9)
NH_4 - N	0.12 (0.03 - 0.30)
TON	0.60 (0.35 - 0.74)
ORTHO-PHOSPHATE	0.012 (0.006 - 0.022)
SALINITY (°/$_{\circ\circ}$)	11.3 (3.9 - 18.5)
SALINITY (°/$_{\circ\circ}$) [Pipe pool]	0.02 (0.016 - 0.300)

* 5 days at 20°C

TABLE 5: Water quality parameters for the river Cree estuary off Creetown Boathouse, and recorded salinities in the Pipe pool.

by the capability of the land most of which is classfied as land with "very severe limitations - use restricted to rough grazing and forestry". Although the Cree flows through pockets of improved land in its lower reaches, in general the harsh geology of the catchment is reflected in the poorly developed agriculture of the area.

Heavy industry is also absent from the sparsely populated Cree catchment and the major causes for concern regarding water quality result from reduced pH's in the feeder streams, the effect of potash and phosphate applications to forestry plantations and the dispersal of effluent from Newton Stewart sewage works (Solway River Purification Board, 1980).

Samples of smelt were obtained from two sampling stations on the river Cree and the sampling dates and number of smelt caught are shown in Table 4.

During the annual spawning migration in March, smelt were obtained from the Pipe pool (OS Sheet 83 GR 416647) located beneath the new A75 roadbridge in Newton Stewart. Tidal influence is strong in this part of the river but salinities are low (see Table 5) and fall within the range of salinities of limnetic water (McLusky, 1981).

Samples of smelt were also collected from the estuary of the river Cree at Creetown Boathouse (OS Sheet 83 GR 465604) some 12 km downstream of Newton Stewart. Water quality parameters for this part of the estuary are shown in Table 5. Data regarding the fauna of the Cree estuary is shown in Table 6 although this list was drawn up from a limited amount of fieldwork on the Cree estuary and should not be regarded as complete. The majority of the fish species recorded in the estuary either occurred seasonally or were present in small numbers. Only smelt, flounders and eels were recorded on each sampling

ARTHROPODA:	*Eurytemora affinis* (Pope)
	Balanus balanoides (L)
	Carcinus maenas (L) *Palaemonetes varians* (Leach) *Crangon crangon* (L)
	Praunus flexuosus (Müller) *Neomysis integer* (Leach)
	Gammarus zaddachi Sexton *Gammarus salinus* Spooner *Corophium volutator* (Pallas)
MOLLUSCA:	*Potamopyrgus (Hydrobia) jenkinsi* (Smith)
PISCES:	Salmon, *Salmo salar* (L) Sea-trout, *Salmo trutta* (L) Eel, *Anguilla anguilla* (L) Herring, *Clupea harengus* (L) Sand goby, *Pomatoschistus minutus* (Pallas) Flounder, *Platichthys flesus* (L) Smelt, *Osmerus eperlanus* (L) Three-spined stickleback, *Gasterosteus aculeatus** (L) Twaite shad, *Alosa fallax** (Lacépède)

* Single specimens

TABLE 6: List of species recorded from the Cree estuary off Creetown Boathouse during this study.

PLATES 1 & 2: Contrasting study sites.

Top: The river Thames off CEGB West Thurrock showing the station loading pier and in the foreground the return culvert for the screen back-washings.

Bottom: The Cree estuary off Creetown Boathouse.

occasion with smelt dominating the catches numerically. Large numbers of herring were recorded in the spring sample but not at other times of the year.

Mean daily air temperatures (max - min/2) for the Cree estuary are shown in Figure 3.

2:2 SAMPLING PROCEDURES

2:2:1 River Thames

Power station intake screens provide a convenient source of biological material for ecological studies (Turnpenny and Bamber, 1982) and have been used extensively for sampling estuarine nekton (eg. Herald and Simpson, 1955; Wheeler, 1968a, 1968b; Wood, 1968; Wheeler, 1969; Huddart, 1971; Huddart and Arthur, 1971a, 1971b; Hardisty, Kartar and Sainsbury, 1974; Moore and Moore, 1976a, 1976b; Van den Broek, 1977; Sedgwick, 1979; Andrews and Rickard, 1980; Turnpenny, Bamber and Henderson, 1981; Andrews, Aston, Rickard and Steel, 1982). In addition, staff at the Central Electricity Research Laboratory have produced a number of research notes dealing with the impingement problem at power stations (Langford, Utting and Holmes, 1977; Turnpenny and Utting, 1980; Turnpenny, 1981a, 1981b; Turnpenny and Utting, 1981; Board, 1982; Turnpenny and Bamber, 1982; Utting and Holmes, 1982).

Cooling water for CEGB West Thurrock is abstracted from the river Thames via a single intake culvert (internal diameter 4.5 m) located under the station pier. Since the ultimate cooling water pipes are only of the order of 25 mm diameter, and because the intake of a large number of fish is ecologically undesirable, the river water must be screened free of suspended material. Large extraneous material is excluded by vertical slats (300 mm apart) arranged around the intake culvert, while finer material (> 100 mm diameter) is removed by 1.9 m wide "Brackett" band screen units (Huddart, 1971). There are six such units each having a capacity under normal conditions of 7.6 m^3/s. The band, which consists of stainless steel mesh with 9.5 mm apertures, rotates at 2 m/s and is continuously back-washed by water jets. The screened material is washed into a discharge trough and is returned to the estuary upstream of the intake culvert.

Langford, Utting and Holmes (1977) have shown that the majority of fish caught at power stations are in the 0+ and 1+ age groups, or are specimens of various small species. However, it remains to be shown whether the size structure of the samples is a result of gear selectivity or a reflection of the value of estuaries as nursery areas. Comparison between screen and otter trawl catches of whiting, *Merlangius merlangus*, at Sizewell power station showed good agreement on two out of three sampling occasions. However, in summer when the power station was operating only half of its plant, the screen samples were much reduced compared to the otter trawl catches. Langford, Utting and Holmes (1977) concluded that further work was needed to clarify the selectivity.

Selectivity of the screen sampling gear might result from mesh penetration by the smaller individuals or an increased ability of the larger individuals to escape from the induced water currents (Turnpenny and Bamber, 1982).

The absence of 0-group smelt from the June and July 1981 samples from West Thurrock might suggest that mesh penetration was a problem until the fish reached a length of 60 mm, the smallest

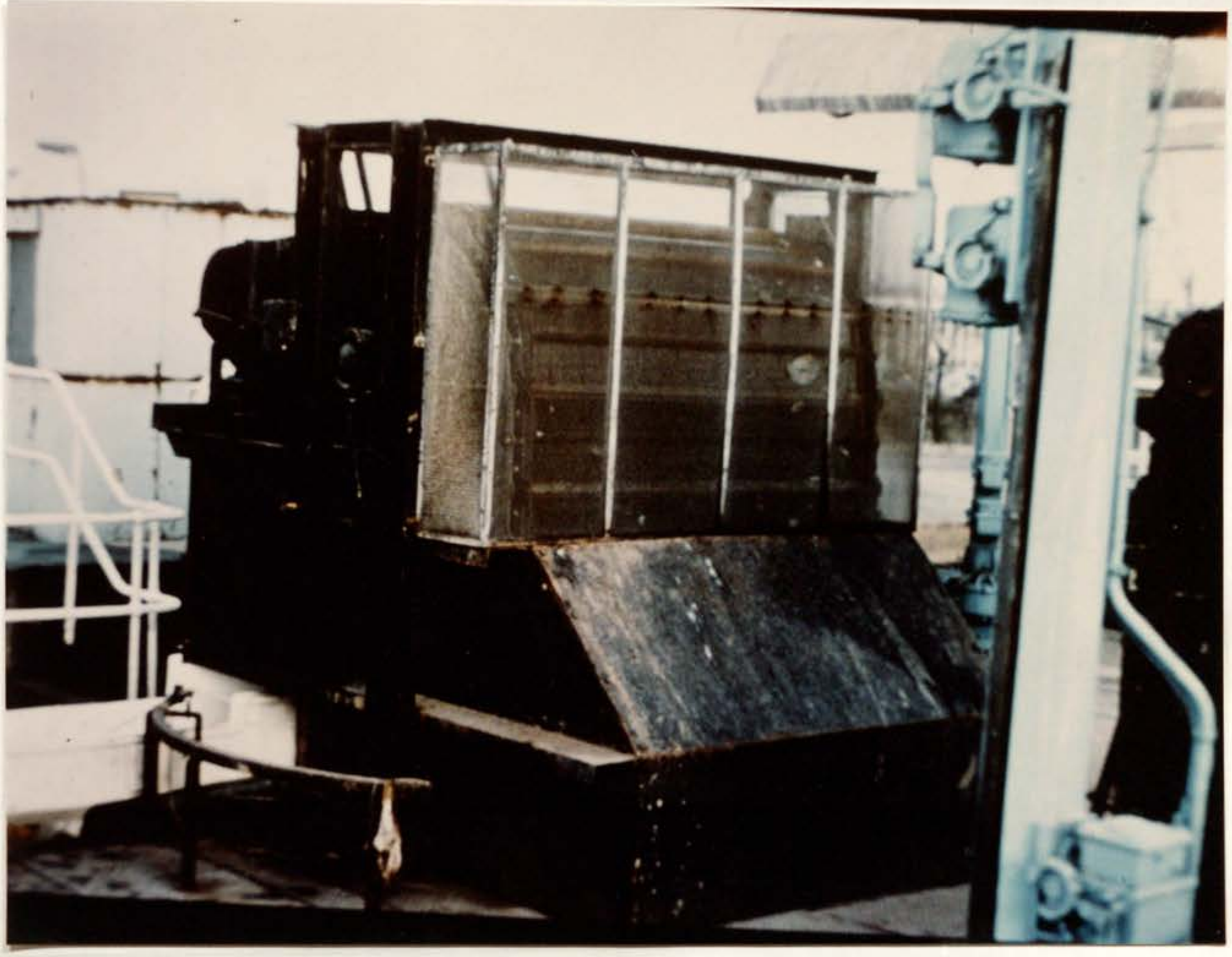


PLATE 3: One of the six "Brackett" band screen units at CEGB West Thurrock.

recorded fork length of smelt at West Thurrock during this study. However, the presence of numerous small crustaceans such as Neomysis integer and Gammarus spp., in the screen catches indicates that mechanisms other than mesh penetration may be responsible. In particular, 0-group smelt may not be present in the estuary off West Thurrock until later in the year (August 1981).

The ability of fish to escape intake into the culverts depends on their swimming performance relative to the intake velocity (Turnpenny and Bamber, 1982). Since swimming performance is related, amongst other factors, to body size (Blaxter, 1969) there may be a source of bias in the samples if larger smelt possess a greater capacity to escape the intake currents. Blaxter (1969) found that the relatively fast species of salmonids and clupeids were able to sustain swimming speeds of 4 body lengths per second or more. The maximum velocity in the intake canal at CEGB West Thurrock is 310 cm s^{-1} and since it is less of a peak load station than the other Thameside generating plants it is orientated to run more or less continuously at high rates (Huddart, 1971). On the basis of these high intake velocities, the peak load nature of CEGB West Thurrock and the small size of Thames smelt (Wheeler, 1979) size selectivity of the gear seems unlikely (Andrews, personal communication). Support for this view is provided by the results of laboratory trials with the sand smelt, Atherina presbyter, which showed that sampling bias caused by escape of the larger individuals was not significant (Turnpenny and Bamber, 1982). Furthermore, the capture of adult salmon, Salmo salar, and a 15 kg conger eel, Conger conger, indicates that even large individuals are susceptible to capture on the intake screens.

Huddart (1971) considered that CEGB West Thurrock was particularly well suited to quantitative sampling since it is situated on a stretch of the estuary that experiences a large, semi-permanent, anti-clockwise swirl which ensures that even species which tend to occur in midstream are represented in the catch. Attempts to compare stream catches with beam trawl catches around the intake culvert to West Thurrock have been unsuccessful as a result of the turbulent water (Andrews, personal communication). However, Huddart (1971) found good agreement between screen catches of large planktonic organisms and the catch of a pump sampler on board a sludge boat.

The screenwell arrangements at CEGB West Thurrock also increases its suitability for nekton sampling. The main operating condition variables of any significance to fish impingement are the cooling water flow rate, the level of chlorination and the number of screens operating (Turnpenny and Utting, 1980). Once within the system, fish have virtually no chance of escape since the tunnel is unlit and provides no visual cues for orientation. Thus factors other than flow rate will only influence the delay from entry to impingement (Turnpenny and Utting, 1980). At CEGB West Thurrock, chlorination is not used so that the fish are still alive when they enter the screenwell and may be able to avoid impingement if they can seek out areas of low turbulence and velocity within the screenwell. This has been identified as a potential source of delay between fish entering the culvert and their being collected in the samples and for sprats, Sprattus sprattus, at Fawley power station the delay was approximately 4 - 5 hours (Turnpenny and Utting, 1980). However, at CEGB West Thurrock the intake culverts enter the forebays vertically and the opportunity for fish to find shelter is reduced since turbulent conditions are present in the screenwells throughout the tidal cycle.

The offshore nature of the intake culvert at CEGB West Thurrock reduces the influence of tidal conditions on the catch. Nevertheless, Huddart (1971) found the catch to be bi-modally distributed with the peaks associated with high and low slack water. Huddart (1971) concluded that the higher catches at high tide were to be expected since the water mass is at a lower temperature, higher salinity and higher oxygen content than at other times. The high catches at low tide were harder to explain but Huddart (1971) suggested that oxygen levels may have been lowest at mid-tide. However, it seems more likely that a concentration effect could be responsible although this effect would be less pronounced than for an onshore intake (Utting and Holmes, 1982).

2:2:2 River Cree

The initial samples of smelt from the river Cree were obtained during the spawning runs in March 1980 and 1981 using a long handled (1.5 m) dip net with a stretched mesh of 38 mm. This technique has been adopted in many studies of spawning run smelt (Rembiszewski, 1970; Murawski and Cole, 1978; Jilek, Cassell, Peace, Garza, Riley and Siewart, 1979) and enables a large number of fish to be collected in a short period of time. Using this method of capture, sampling was carried out on each day of the spawning runs so that temporal variations in sex ratio and size distribution could be investigated.

Further sampling was planned for the spawning run in March 1982 but high water conditions disrupted the normally well synchronised run and samples could not be obtained. However, a number of mature adults were collected and transported back to the laboratory for stripping.

The cessation of feeding by adult fish during the spawning run and the absence of 0-group fish amongst the migrants necessitated the initiation of an estuarine sampling programme. Furthermore, Bailey (1964) considered that "while spawning run smelt have been investigated extensively, few studies have included samples obtained at other times of the year."

On the basis of evidence provided by salmon netsmen along the Cree estuary, a preliminary seine netting was carried out at Creetown Boathouse on 11th June 1981. The seine net used was 61 m long and 8 m deep in the middle, tapering to 1.6 m in the wings. The mesh size was 35 mm in the wings and 10 mm in the bag (stretched mesh). This netting proved to be unsuccessful but served to highlight the limitations of this technique.

Firstly, in order to fish such a net a sturdy boat was required and while the salmon netsmen's coble was available during the weekly close time through the season (March 1st - September 15th) no samples could be collected outside this period. Secondly, the mode of action of the net, its fine mesh and the nature of the estuarine sediments rendered the netting process labour intensive. Since assistance could rarely be guaranteed a method of capture that could be operated by only two people, from a small inflatable dinghy was to be preferred.

Monofilament gill netting appeared to satisfy these requirements since manpower for the handling of such nets is low and almost any size of boat can be used for fishing with them (Von Brandt, 1975). However, there are drawbacks to the use of this kind of gear:

i) The recovery of fish from the netting can be difficult and the method is not therefore recommended where large catches are anticipated (Von Brandt, 1975). Furthermore, large scale sampling was to be avoided on ecological grounds.

ii) Gill nets are highly selective.

The netting procedure adopted involved anchoring the net at both ends just prior to slack water (low tide) and fishing the entire width of the estuary as the tide flooded. The net was only fished for approximately 10 minutes into the flood thereby avoiding excessively large catches. Even so, catches of up to 100 smelt were recorded.

The problem of size selectivity was minimised by the use of a survey type gill net (Lundgrens Fiskredskaps-Fabrik, Stockholm, Sweden) which was 122 m long, 1.8 m deep and comprised eight 15.2 m long panels of 8, 10, 12.5, 16, 19, 22, 25 and 30 mm mesh (bar measure). However, the need to anchor the net (to avoid fouling on the stone breakwaters) meant that the smallest and largest mesh sizes inevitably fished the inter-tidal zone rather than the main stream. The small number of 0-group fish in the samples could be a manifestation of this phenomenon. Bobzin and Finnern (1969) (in Von Brandt, 1975) recommended mesh sizes in the range 12 - 18 mm for commercial gill net fisheries for smelt in Europe. It seems unlikely, therefore, that size selection precluded the capture of adult Cree smelt.

Ease of netting was facilitated by fishing only at times when low freshwater flows corresponded with neap tides.

2:3 TREATMENT OF MATERIAL

Immediately after the smelt were removed from the fishing gear all those individuals which were not killed during capture were rendered unconscious by a sharp blow to the head in order to prevent regurgitation of their stomach contents when placed in the preservative. In the case of Thames smelt, approximately 50% survive entrapment on the screens but are stunned upon capture (Andrews, personal communication). In the Cree, all fish were alive upon capture and were rendered unconscious as described above.

Post-mortem digestion of the stomach contents was minimised and rapidity of fixation was ensured by opening up the coelom with a mid-ventral incision in the area between the paired fins, immediately after death (Windell and Bowen, 1978). The fish were then placed in sealable plastic containers, covered in a 4% aqueous solution of formaldehyde and transported to the laboratory.*

In the laboratory, the fish were removed from the preservative and washed thoroughly in circulating water for approximately 24 hours. They were then drained of excess water, blotted dry and the lengths of the fish from the tip of the snout to the tip of the median rays of the tail (fork or median length ± 1 mm), and from the tip of the snout to the end of the caudal fin (total or absolute length ± 1 mm) were determined using a standard 400 mm measuring board. The measurements were taken in a straight line with the mouth of the fish closed and in the case of total length with the caudal rays squeezed together to give the maximum length (Lagler, 1956). The fork length was used in preference to the total length since in older fish, or fish subject to fin rot, the edges of the caudal fin may become ragged and the measurement subject to inaccuracy (Williams, 1963). Paired values of fork and total length measurements were then used to establish a relationship which facilitated the comparison of data from this study with that of other workers who preferred total length measurements (eg. Warfel, Frost and Jones, 1943; Bailey, 1964). The regression

* Via GPO from CEGB West Thurrock (approximately 2-3 weeks in preservative but up to 2 months). Direct by car from the river Cree (3-4 days in preservative).

lines were described by the equations:

Total length = 1.080 Fork Length + 3.21 $r = 0.989$ River Thames

Total length = 1.057 Fork Length + 6.12 $r = 0.978$ River Cree

Care had to be exercised when dealing with early references since the terms 'total' and 'fork' length were often used synonymously (Lagler, 1978).

The coelom of the fish was then opened up completely by means of a mid-ventral incision and excess fluid was allowed to drain out of the abdominal cavity. After blotting dry, the fish were weighed (total weight ± 0.1 g) on a centre pan laboratory balance (Sartorius 1000 g, Sartorius - Werke Ag, Gottinger, Germany). The sex of the fish was then determined and the gonads were removed and weighed separately (gonad weight ± 0.01 g). Care was taken to ensure that the same measurement technique was used for each fish.

Ova from gravid females were placed in numbered vials containing Simpson's (1951) modification of Gilson's fluid and stored for enumeration at a later date. In the case of hermaphroditic individuals the ovotestes were stored in 4% formalin for histological examination at a later date.

The complete digestive tract was also removed from each fish and placed in a separate numbered vial containing 70% ethanol. All vials were then stored out of direct sunlight.

Scale samples were removed from the side of the fish in the area between the lateral line and the origin of the dorsal fin. This region of the fish was selected since the scales in this area are large and symmetrical although in some cases this area had been completely descaled. This phenomenon was more common in the samples from the river Thames and was probably a result of the physical forces involved in screen sampling, combined with the deciduous nature of the smelt scale which is attributable to the shallowness of their scale pockets (Van Oosten, 1957). Huddart and Arthur (1971b) also found a tendency for fish to become descaled while passing through the screens and they therefore advocated the use of otoliths for age determination. However, the problem was never so severe in this study and in the vast majority of cases readable scales were present on the shoulder region. Where the shoulder region had been totally descaled, scales from the base of the dorsal fin were usually still present. These were used to age the fish but not for back-calculations. The scales were removed individually from the fish using either pointed forceps or a hypodermic needle, since this technique resulted in cleaner scales than a 'scrape' sample and eliminated the need to remove mucus and epidermal tissue prior to viewing. Approximately 6 - 10 scales were taken from each fish and mounted in a drop of water on a microscope slide. A cover slip (22 x 22 mm) was then placed over the scales and sellotaped at each end to the slide. The slide was numbered and viewed at a later date.

The methodology described above was adopted for all samples taken from the estuarine environment of both the river Thames and the river Cree. Because of the large sample size of spawning run fish from the river Cree in both 1980 and 1981, it was considered impractical to transport all of the fish back to the laboratory in preservative. In this case, the fish were weighed and measured as described above but fresh weights and lengths were recorded. Since it has been shown that most preservatives affect the length and/or the weight of fish (Billy, 1982) a correction factor must be applied to either the preserved or fresh data sets to render them comparable. Although several studies have been carried out on the magnitude of the changes after preservation (eg. Van Oosten, 1929; Burgner, 1962; Parker, 1963; Stobo, 1972; Billy, 1982) most of these studies employed 10% formalin as the preservative. In order to gain some insight into the effects of preservation in a 4% solution of formalin, a small scale experiment was carried out using 10 spawning run smelt in the size range 202 - 253 mm. Each fish was tagged using a numbered polythene double attachment trailer tag, and then weighed (total weight) and measured (fork length), as described previously, before being placed in a 4% formalin solution. The fish were removed from the solution daily and re-weighed and re-measured. After two weeks only minor changes were detectable in both length and weight and the experiment was terminated.

The results showed that while there was a shrinkage in the length of the fish amounting to 3.3% (range 1.6 - 4.7%) the weight of the fish increased by an average of 8.4% (range 7.2 - 9.3%) following two weeks of preservation. This result agrees closely with a similar study by Parker (1963) who found that a 3.8% formalin solution resulted in a 4% shrinkage in length of juvenile Oncorhynchus spp. The results of other studies on the effects of preservation have been summarised by Billy (1982).

The results derived from this experiment were used to correct the length and weight of spawning run fish so that the data was comparable with preserved specimens. While it is appreciated that fresh lengths and weights are more meaningful than preserved values, the larger number of computations involved in converting the preserved data to fresh weight and length equivalents, and the possibility that

0-group specimens may have responded differently to preservation (as described by Billy, 1982), favoured the adoption of preserved equivalents for all data.

The food habits of spawning run fish were examined by taking sub-samples of fish back to the laboratory after preservation in the manner described for estuarine samples.

CHAPTER 3: DISTRIBUTION AND COMMERCIAL VALUE OF THE RESOURCE

3:1 INTRODUCTION

During the formulation of a research proposal, and the subsequent literature search, for this study, it became apparent that the commercial fisheries for smelt in Britain had undergone a considerable demise. At the turn of the century, the species was highly regarded as a food fish (Masterman, 1913) but today its commercial value is negligible.

The short-cycle nature of the life history, characterised by high productivity, early maturation and the rapid accumulation of biomass in any year class renders the smelt "a most promising species for commercial exploitation" (Kriksunov and Sidorin, 1975). However, the British fisheries have suffered from a lack of management and legislative protection and since the spawning stock is only composed of two dominant year classes, overfishing can easily result in the collapse of the population. Mann and Mills (1979) described the collapse of the Pacific sardine, Sardinops caerulea. This species normally has seven or eight year classes spawning together, but overfishing in the 1930's and early 1940's effectively reduced this to two. Subsequent poor recruitment resulted in the collapse of the population.

The objectives of this chapter are to review the past and present commercial status of the smelt in Britain; to identify any shortcomings in the legislation designed to protect smelt stocks and to investigate the possibilities for management and improvement of stocks in those rivers where the species has suffered a decline. Valuable information regarding the distribution of the smelt in Britain is presented in Figure 4 together with Maitland's (1972) distribution map. Table 7 lists the rivers from which smelt were recorded in this study.

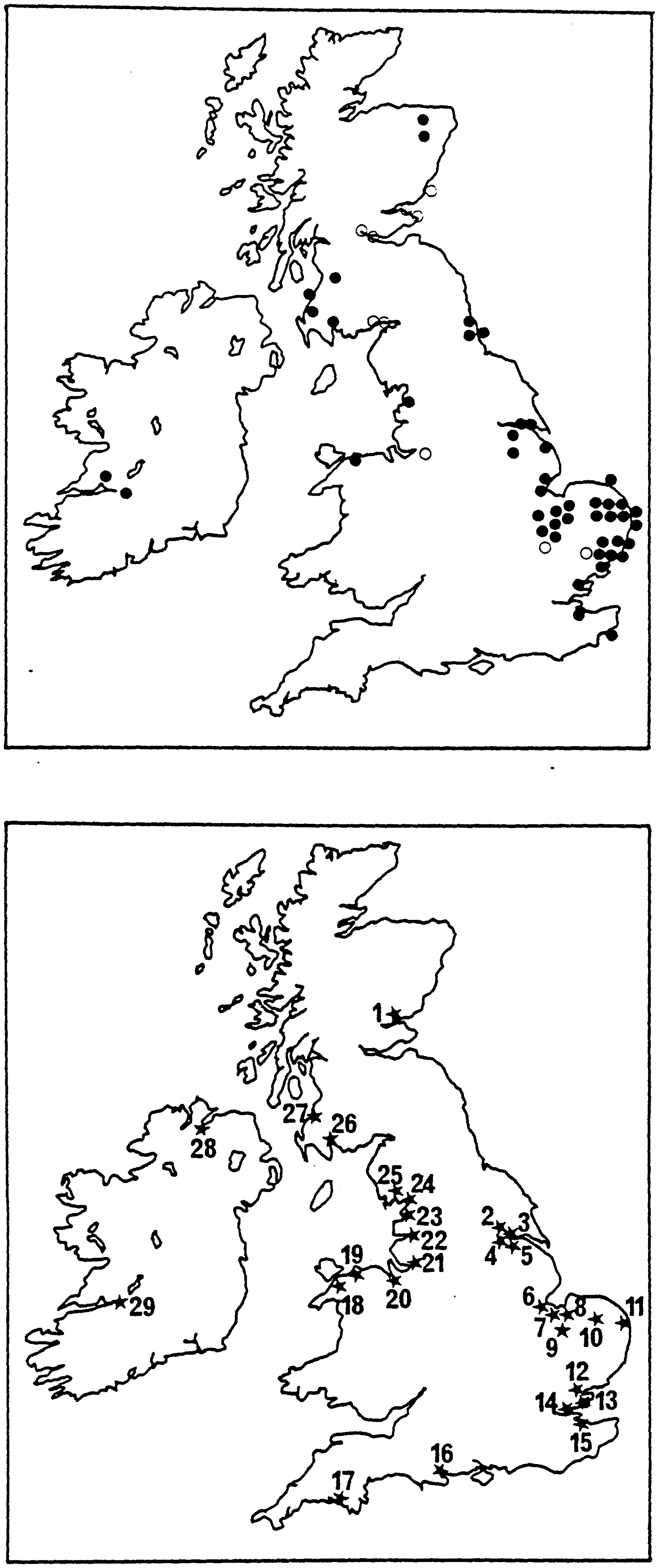


FIGURE 4: The distribution of smelt in Britain.

Top: From Maitland (1972) [○ records prior to 1960; ● records after 1960]

Bottom: Data derived from the present study (see Table 7).

1. River Tay
2. River Derwent
3. Welton Ponds (river Humber)
4. River Ouse
5. River Trent
6. River Welland
7. River Nene
8. River Ouse
9. New Bedford river
10. River Wensum
11. River Yare (Breyden water)
12. River Blackwater
13. River Crouch
14. River Thames
15. River Medway
16. River Piddle (single specimen only)
17. River Tamar
18. River Seiont (unsubstantiated)
19. River Conway
20. River Dee
21. River Mersey (Manchester Ship Canal)
22. River Ribble
23. River Lune
24. River Kent
25. River Leven
26. River Cree
27. River Stinchar
28. River Foyle
29. River Shannon

TABLE 7: Rivers from which smelt were recorded during the course of this study.

3:2 METHODOLOGY

The information presented in the following results section is a collation of data collected by correspondence and from a review of the literature. The author is grateful to all organisations who supplied information (Appendix 1), some of which was only uncovered after considerable research. The views expressed are those of the individuals quoted and not necessarily the parent Authority.

The information is presented for England and Wales (according to Regional Water Authority boundaries), Ireland and Scotland individually.

3:3 RESULTS

3:3:1 England and Wales

(i) Anglian Water Authority Area:

Southwell (1887a) reported that for many years a successful and frequently remunerative smelt fishery had been prosecuted in Norfolk waters although never of such significance as to appear in fishery returns.

The river Ouse had an ancient smelt fishery, based on spawning run fish, a single share in which could produce as much as £50. At Yarmouth and Lowestoft, large quantities of smelt were taken annually and in autumn good smelt angling was possible from piers using shrimp as bait. The greatest commercial fishery existed in the shallows and creeks of Breydon, where 10-12 boats fished between 1st September - 30th April. Fishing also extended up the Waveney, Yare and Wensum but was of little significance in the North river or Bure. Rudd (1936) reported that the yield of smelt was enormous with several families dependent upon the fisheries for a great part of their living and there was even a smelt netters society.

The capture of large numbers of smelt however, and the pollution of the river Wensum, were causes for concern at the time of Southwell's (1887a) writing, and Rudd (1943) stated that smelt "formerly came upstream in thousands but now only a few ascend our [Norfolk] rivers".

Today runs of smelt occur up the tidal Ouse and the New Bedford river as far as Earith. The fish are mostly observed when mature fish die in numbers in April or May every second or third year. Smelt are also occasionally caught in the non-tidal river Nene and although occasionally recorded in the Spalding area, they have not been recorded in the non-tidal reaches of the river Welland in the last ten years. There are still occasional strong runs of smelt to the head of the tide in the river Wensum and small numbers occur in fishery surveys in other Broadland rivers and are occasionally taken by anglers (Linfield, personal communication). The only 'commercial' fishery for smelt in Norfolk waters occurs at Breydon on the Yare where 3 - 4 tons are netted annually for use at the Otter Trust (Wortley, personal communication).

(ii) Northumbrian Water Authority Area:

Howse (1890) recorded smelt from the Tyne at Elswick and found them to be frequent visitors to the Tees in certain seasons. Wallis (1769) stated that "that admired little fish, the smelt, is taken in great abundance in the Tyne and in our other rivers towards the sea".

Today, however, Northumbrian Water Authority have no records of any smelt populations within their area (Walker, personal communication).

(iii) North-West Water Authority Area:

Smelt formed the basis of a cottage industry in several Cumbrian rivers with the fish being seined (1" mesh) each spring in the rivers Duddon and Leven. Catches were never high but an old saying that "a cigar box full of smelt is enough for a weeks wages" suggests that they didn't have to be. In Victorian times, those who could afford smelt were prepared to pay half a guinea per pound (Evans, personal communication).

Of particular interest was the landlocked population of smelt in Rostherne Mere, Cheshire, which was known to have inhabited the lake since the early eighteenth century (Coward, 1912a). Day (1884) believed the smelt to have been introduced to the Mere, but Coward (1912b) didn't place "much faith in this remark" and considered smelt to have been present in the Mere since it was possible for them to ascend from the sea ie. prior to the building of weirs.

Coward (1924) found a single specimen of the Rostherne smelt on March 31st 1922, and concluded that the species was still surviving. However, it seems probable that the population died out during the 1920's. Netting in the Mere by Ellison and Chubb (1963) failed to reveal any smelt and Maitland (1979) considered that increased eutrophication would make re-establishment of the population difficult.

In 1979, smelt were recorded from the Mersey estuary (in the tidal Manchester Ship Canal) and from the Ribble estuary downstream of Preston (Cragg-Hine, personal communication). They are also present in the Lune estaury downstream of Lancaster (Gardiner, personal communication) and sizeable spawning runs of smelt have been recorded from the river Kent in recent years (Durie, personal communication). Hardy (1968) also found smelt runs into the tributary estuaries of Morecambe Bay although survey seine nettings in the Leven and Kent estuaries in 1980 only revealed an average number of < 1 (11 nettings) and 5 (6 nettings) smelt for each river respectively (Evans, personal communication).

The commercial value of the smelt today is nil and when they do appear in local shrimp and whitebait fisheries they are regarded as a trash species.

(iv) Severn-Trent Water Authority Area:

In the records of the Borough of Nottingham dating from the fourteenth century, Easton (1979) found the following passage:-

> "John, Constable of Chester, bestowed upon the Church and Monks of Lenton the first draught of sparlings next after the draught of his steward in the said fishery".

Easton (1979) showed that by 1890 however, the smelt did not appear in the species list for the Trent and he attributed the decline to the use of decreased mesh sizes to catch fish for food, and/or estuarine pollution.

By 1962, it was considered that no species of fish could survive in the Trent below Gainsborough because of the anaerobic conditions. Since the early 1960's improvements in the Trent have resulted in the re-establishment of a stable fish population including smelt which were recorded in 1978 in considerable numbers (Easton, 1979).

The present position regarding the recovery of the smelt population in the Trent is unclear due to changes in the screening arrangements at a local power station which have reduced its efficiency as a fish sampler. The smelt has not been recorded from the river Severn (Sedgwick, personal communication).

(v) Southern Water Authority Area:

Commercial fisheries for smelt existed in the Medway estuary between Rochester and Sheerness in the 1920's and 1930's but by the 1950's the species was scarce in the river (Wheeler, 1979) and only taken in small numbers (Van den Broek, 1980).

The estuary is now heavily polluted and has been for a good many years and only occasional smelt are recorded. There are no records of smelt in the other rivers within the Authority's area (Joslin, personal communication).

(vi) South-West Water Authority Area:

Although no historical records of smelt are present for the area covered by this Authority, and they have not been recorded by the Authority in recent times, smelt have bred regularly in the Tamar since 1968 (Dando, personal communication). No commercial fishery exists in the river and it would be unpopular because of salmon and sea-trout runs.

(vii) Thames Water Authority area

The fishery for smelt was probably one of the oldest (smelt bones have been identified in several layers dating from Roman Southwark) and most important of all the tidal Thames fisheries (Wheeler, 1979).

A newspaper clipping from 4th April, 1797 (quoted by Wheeler, 1979) illustrates the magnitude of the fishery:-

> "Smelts have been so plentiful in the river lately that on Wednesday the fishermen disposed of them on the banks of the Thames at the rate of 2d a basketful, containing near 100; and on Monday in Deptford Creek, the draught was so great that they were sold in the manner of sprats, by coal measure..."

Ormsby (1928) found evidence that up to around 1810 50000 smelts were caught and taken daily to Billingsgate market, and up to 3000 smelt were taken in a single haul. At its peak, the Thames smelt fishery supported 30 boats.

By 1828 however, the fishery had been severely reduced (Ormsby, 1928) and the decline in smelt appeared to be concomitant with deteriorating water quality (Yarrell, 1836) particularly reduced dissolved oxygen levels (Huddart, 1971). Wheeler (1979) also believed that illegal whitebait nets had contributed to the decline of the smelt.

By the end of the nineteenth century smelt were only fished for commercially at the mouth of the Thames although, as reported by Murie (1903), they still progressed upstream in some years, presumably when periods of increased freshwater flow resulted in improved oxygenation of the river.

Today the smelt is found throughout the river and is abundant in the middle estuary (Andrews et al, 1982). As early as 1969 Wheeler (1969) believed there to be a sufficient population in the Thames estuary to give rise to a smelt run in the Thames and he also found smelt to be common in the neighbouring rivers Crouch and Blackwater.

However, the species was still rare in the Thames in 1974 but showed a marked increase in abundance by 1977. Annual peak counts of smelt per 100 x 10^6 gallons of cooling water used at West Thurrock were 3 (1974), 14 (1975), 44 (1976), 972 (1977), 1029 (1978) and 2484 (1979) (Andrews et al, 1982).

The species is not however exploited commercially in the Thames today (Armstrong, personal communication)

(viii) Welsh Water Authority Area:

Since 1975, the smelt fishery in the Conway, which used to be a remunerative fishery, has declined considerably. Catches of 30-40 dozen smelt (50p per dozen) used to be common place over a period of four hours fishing, but in 1978 the last year of the fishery, very few fish were taken. Smelt were also caught by netsmen in small numbers in the Dee (5 - 10 years ago) and the Seiont (7 - 8 years ago) although this latter report has not been substantiated by bailiffs (Jones, personal communication).

The population in the Dee still appears to be sizeable and smelt are quite abundant in the canalised semi-freshwater section during spring tides (Pearce, personal communication).

(ix) Wessex Water Authority Area:

Records of smelt on the south coast of England are very rare but a single specimen was caught in a smolt trap in the river Piddle, Dorset in 1975. Several reports of smelt being common in Poole harbour have arisen from confusion with the unrelated sand smelt, *Atherina presbyster* (Solomon, personal communication).

(x) Yorkshire Water Authority Area:

The smelt was taken in various Yorkshire rivers during the last century and were so abundant in the Ouse in December 1834 that they were sold in the Leeds market at 2^d per pound (Howse, 1890).

Clarke and Roebuck (1881) recorded smelt as being common in the estuaries of the Tees and Humber and they abounded in the Ouse.

Today, smelt have been recorded in the river Ouse and river Derwent and there have also been reports of captures in the British Sugar Corporation settling ponds which are close to the Ouse (the fish may have been washed in during a flood). It would appear that smelt are also present in the Humber (they have been reported in the past from the Market Weighton Canal) and they have been reported in Welton ponds on the edge of the Humber (Cresswell, personal communication), where they often appear in anglers catches (Harrison, personal communication).

3:3:2 Ireland (including Northern Ireland):

Modern authorities are mostly silent as to the distribution of smelt in Ireland and in the past the distribution has been confused by records including <u>Atherina presbyter</u> (Kennedy, 1948).

The only record in Northern Ireland is based on samples of smelt obtained from the intake screens of Coolkeeragh power station on the banks of Lough Foyle at Londonderry (Vickers and Watson, 1973).

Smelt are plentiful in the river Shannon and are well known to local fishermen who are familiar with it down the estuary. In March smelt ascend to Limerick and occasional specimens are caught on worms by trout anglers and by youngsters in landing nets or even their bare hands when the shoals are closely packed (Kennedy, 1948).

The Shannon and Foyle are the only authenticated Irish records although Regan (1911) was of the opinion that smelt probably occur throughout Northern Ireland. However, nets which should catch smelt have been used at various times in most of the river estuaries in Ireland and the absence of records together with the absence of any commercial fishery suggests that the species is not resident elsewhere in the country (Moriarty, personal communication).

3:3:3 Scotland

The major smelt fisheries occurred in the Firths of Forth and Tay, and in the Solway Firth.

In the Firth of Forth, near Alloa, smelt were taken in great numbers especially towards the fall of the year. In March, the species ascended the Forth and spawned approximately two miles below Stirling Bridge (Parnell, 1838). At this time, the species provided an abundant food for the poorer people of Stirling (McLusky, 1978) and was also in demand as a luxury food for the table, receiving a ready sale at the Edinburgh market (Parnell, 1838).

Smelt were also abundant at Crammond on the Forth. Sinclair (1779) wrote that:

> "the Amon formerly abounded with a variety of fish such as trouts, grilses, some salmon and great plenty of smelts, but owing to liming of the adjacent grounds and watering flax in the river it was for some years almost totally deserted by these different kinds of fish which are still extremely scarce".

Smelt continued to be exploited in the Forth off Alloa until the 1950's when pollution resulted in a considerable decline in the smelt stocks. Prior to this up to 100 lbs. of smelt could be taken in one sweep during September - March, but the fishery had totally collapsed by 1957 (Bremner, personal communication) and the species no longer occurs in the Forth (Elliot, personal communication).

Smelt also occurred in the Tay estuary (Parnell, 1838) and were the subject of a commercial fishery (Holden, personal communication). However, by 1970 the commercial fishery had virtually collapsed although a mixed fishery of smelt and whitebait amounting to 46 cwt. still exists (Clarke, personal communication).

Populations of smelt also occurred in the tidal reaches of the rivers Esk, Nith, Annan, Urr and Cree which drain into the Solway Firth (Service, 1902; Truckell, 1968).

By the time of the Royal Commission on Tweed and Solway Fisheries (1896), the state of the smelt fishery in the Solway showed "a great deterioration". In the Annan particularly, the decline was such that whereas thirteen sparling nets used to operate at Annan Waterfoot none were fishing in 1896 because "undoubtedly there are no fish [smelt] to get" (HMSO, 1896). In the Nith, a similar decline was evident and one witness who spoke to the Commission was quoted as saying "it is only bosh to say they are worth fishing for now but at one time since they were very productive". A similar decline was evident in the remaining Solway rivers although the evidence was less discouraging regarding the Cree but "still it shows that it is not what it used to be" (HMSO, 1896).

By the turn of the century, Service (1902) wrote that in the Esk, Annan, Urr and Nith the smelt was hardly known as a freshwater fish and they had declined greatly in the estuary.

Today the smelt population in the Inner Solway Firth appears to be almost non-existent and the species no longer occurs in routine trawls in the area (Perkins, personal communication). The only remaining commercial smelt fishery occurs on the river Cree during the annual spawning run. Until recently this fishery was executed with only a modest degree of success using a salmon seine net, but the acquisition of a small mesh sparling net greatly increased the efficiency of the operation and in 1983 the netsmen removed 4 tonnes of spawning run smelt in two days.

On the Ayrshire coast smelt have been recorded in the Stinchar and the Girvan. The very few fish in the Stinchar have no commercial value today (Wilson, personal communication) and in the Girvan the smelt is virtually unknown because of the extreme pollution in the lower reaches. A few smelt are sold at the Ayr fish market where they achieve a price of £2 per stone (Grey, personal communication).

To the north of the Ayrshire rivers one smelt was recorded in the Firth of Clyde off Brodick by Elliot, Lowrie and Murdoch (1901), and Maitland (1972) reports the occurrence of smelt in the Lugar water. Reports of smelt from Oban Bay were dismissed as confusion between smelt and Atherines by Smith (1895), and Buckley and Harvie-Brown (1891) dismissed reports of smelt in the Outer Hebrides for the same reason.

On the East Coast, Howse (1890) recorded smelt infrequently in the Tweed, but they are not caught today (Berwick Salmon Fisheries Company, personal communication).

No evidence could be found of any smelt population north of the Tay although Maitland (1972) recorded smelt in the rivers South Esk, Ythan and Deveron. In the case of the latter named river there no longer appears to be a population of smelt (Gray, personal communication).

3:4 DISCUSSION

While the nature of this study prevents any detailed analysis of the status of the populations of smelt in Britain, it is clear that the commercial value of the smelt has declined such that the species is hardly known as a commercial fish today.

Masterman (1913) considered that the collapse of the commercial smelt fisheries was a result of over fishing and/or pollution, but believed that by imposing rational regulations and restrictions the fisheries could be improved and developed. Jenkins (1925) while agreeing that the species was susceptible to over fishing believed that the existing close seasons and mesh limitations, if adhered to, would act as regulators. However, the legislation applicable to smelt fisheries in Britain appears to have suffered from severe drawbacks.

The earliest record of legislative protection designed to protect smelt stocks dates back to the reign of Elizabeth I who imposed a mesh limitation . George II rendered it penal to take or possess "any smelt not 5" long" (Southwell, 1887b). The degree to which these regulations were enforced is questionable however, and both Southwell (1887a) and Wheeler (1979) attributed the decline in traditional smelt fisheries at least partly to the capture of young smelt by whitebait fishermen. The information provided by Harding (1882) suggests that shrimp fishermen were also responsible for the destruction of large numbers of young smelt and Lillelund (1961) found that the shrimp fisheries on the river Elbe took double the amount of smelt that was taken by the smelt fishermen.

Other legislation which was used to regulate smelt fisheries included the Norfolk and Suffolk Fisheries Act, 1877, which was used

District of Local Fishery Committees:		
Northeastern	-	21 July - 21 March
Eastern	-	1 April - 31 August
Milford Haven	-	1 March - 31 August
Lancs. & Western	-	1 April - 31 October
Cumberland	-	1 February - 1 September
District of Boards of Conservators:		
Ouse, Nar, Nene	-	1 April - 31 August
Yare, Waveney, Wensum	-	10 March - 12 May
Dee	-	1 April - 31 October
Kent & Bela	-	1 April - 31 October
Thames	-	25 March - 27 July (size limit = 6")
Other Close Times:		
Rochester	-	1 April - 30 June (mesh size & net limitations)
Forth	-	30 April - 31 August
Thames (Imposed in 1630 by the Lord Mayer Sir Robert Ducie)	-	10 March - 14 September (West of London)
	-	21 October - Good Friday (East of London)

TABLE 8: The close seasons for smelt in several districts (modified from Masterman (1913)).

to regulate the large Norfolk fisheries, and the Solway Act, 1804 which was applicable to the Solway fisheries. However, these Acts were rarely enforced and the only reference to a Court action which could be discovered in the literature referred to the charging of two Creetown men under Section 9 of the Solway Act at Wigtown Sheriff Court in 1890 (HMSO, 1892). Smelt were also protected locally by various close seasons which are listed in Table 8.

Masterman (1913) considered that in many instances close seasons for smelt were designed not to protect smelt over the spawning period but to prevent fishing for smelt during the months when salmon smolts might be migrating.

The degree of legislative protection afforded to smelt fisheries was summarised by Southwell (1887b) who stated that

> "...the amount of interest shown in the smelt fisheries of the UK, either by imperial or local authorities, is small indeed and this delicate and delicious fish is from utter neglect and unfair treatment becoming lost as a source of food and profits in the localities where it formerly abounded".

The Solway White Fishery Commission (1892) recommended a close time for smelt extending from 1st February - 1st August, which would protect the smelt and the salmon smolts but since the revenue from summer smelt fishing was low anyway would not be too severe a financial restriction. However, the Solway fisheries had already suffered severe decline and the recommendation was never enforced.

The reasoning behind such a close time is sound and is based on the need to protect breeding and ripe fish, particularly when the fish are confined in large numbers within narrow limits, as during the spawning migrations of smelt. Unfortunately, the most valued smelt are mature individuals full of roe and a total ban on exploitation of fish returning to spawn would be out of line with the protection applied to other anadromous salmonoids and must be regarded as un unduly harsh restriction (Masterman, 1913). Furthermore, exploitation of smelt on the spawning grounds prevents the destruction of large numbers of juvenile fish, which remain in the estuary at this time. Kendall (1927) considered that if seine netting was carried out in the estuaries using nets of a mesh size capable of catching adult smelt, large numbers of juvenile smelt would also be taken in the net and destroyed when the net was hauled.

Exploitation on the spawning grounds however, must be carefully regulated having due regard for the fundamental biological requirements of the species. Manipulation of the period of exploitation to enable sufficient spawning escapement may be of value in this respect. For example, Hoover (1936) showed that marked changes in sex ratio occurred during the spawning migration and that by monitoring these sex ratios exploitation could be confined to the period of male domination. The results presented in Chapter 5 show that similar changes in sex ratio occur in the Cree population.

The commercial value of the species may be enhanced by re-introducing smelt to those rivers where over fishing has resulted in the decline of the population. As early as 1892, the view was expressed that:-

> "...the attention of the Fishery Board of Scotland might be directed to the introduction of this excellent fish in estuaries where at present they do not exist, such as those of the Luce and Poltanton, both within the limits of the Solway" (HMSO, 1892).

Furthermore, in a letter to Professor Baird in America, Harding (1882) inquired as to the suitability of smelt for artificial

PLATE 4: Hand stripping a mature female smelt from the river Cree.

propagation since he was of the opinion that "the artificial propagation of them [smelt] in large quantities would be beneficial to the fisheries."

Bigelow and Schroeder (1953) concluded that the smelt

> "has proved a favourable fish for artificial hatching and large numbers of fry are so produced yearly in Massachusetts"

and it has been

> "proven possible to re-introduce smelt by introducing the eggs or fry into streams from which it has been extirpated".

Results from the egg incubation experiment (see Chapter 5) show that smelt eggs can be stripped, fertilised and hatched out using inexpensive equipment. Mean percentage hatches of between 10% - 27% were obtained but up to 53% hatch was recorded. Hatching successes of up to 80% were achieved by fertilising the ova using the 'wet' technique and allowing water to distribute the eggs in seed trays. In this manner the eggs became thinly distributed and dead eggs could readily be handpicked without damaging neighbouring live eggs.

These results suggest that the re-establishment of smelt populations, and ultimately commercial fisheries, in the rivers where smelt no longer occur, or have declined, should be possible with a minimum of investment.

CHAPTER 4: AGE AND GROWTH

4:1 INTRODUCTION

In the 250 years that have elapsed since Hans Hederström first determined the age of pike from vertebral growth rings, many techniques of age determination have been developed. Ricker (1975) believed the various techniques to be so diverse that "few kinds of fish in temperate waters can hope to conceal their age from a persistent investigator". The resultant age data, in conjunction with length and weight measurements, can provide information on stock composition, age at maturity, life-span, mortality and production (Bagenal and Tesch, 1978) as well as growth rates.

The objectives of this chapter are to investigate the longevity, condition and growth rate of smelt and to identify any variations between study sites. When combined with the data provided by Masterman (1913), the results of this study should provide valuable information regarding the life history of British smelt populations and enable comparisons with other populations of smelt, *Osmerus spp.*, from mainland Europe, Asia and North America.

4:2 METHODOLOGY

4:2:1 The Use Of Smelt Scales In Age Determination

The structure of the smelt scale is very specific (Belyanina, 1969) and singularly adapted for age determination (Masterman, 1913). With the exception of the occasional use of vertebrae (Nordquist, 1910), otoliths (Cumaevskaja-Svetovidova, 1945) (in Belyanina, 1969) and various other bony elements (Marre, 1931) (in Belyanina, 1969) all other studies involving ageing of smelt have relied upon scale analysis.

Masterman (1913) identified three distinct forms of circuli on smelt scales.

i) Spiral circuli which commence abruptly a short distance from the centre of the nucleus and travel round in a spiral fashion. These circuli are confined to the central portion of the scale and, as also recorded by Masterman (1913), they were only occasionally identified from the scales of Thames or Cree smelt.

ii) Concentric circuli which are formed in complete circles, ovals or other more irregular ovoids. In the majority of scales, the first circulus is formed as an ovoid ring and is succeeded by a series of regular concentric circuli. The majority of the circuli on scales from Thames and Cree smelt were of this type.

iii) Bilateral circuli occur about the median or antero-posterior axis of the scale and are in the form of incomplete rings, the free ends of which face the posterior edge of the scale. These circuli were entitled incomplete rings by McKenzie (1958) and horse-shoe rings by Bailey (1964).

The appearance of spiral, concentric and bilateral circuli can be seen in Plates 5, 6 and 7.

Bailey (1964) defined a growth field as a series of complete circuli followed by a series of horse-shoe circuli that gradually shorten as growth slows down. The first circulus that appears in the following growth season cuts across the shortened circuli and constitutes the annulus. In this manner, a real morphological age distinction is produced, whereas determination of age based on the spacing of the circuli would be extremely difficult (Masterman, 1913).

Masterman (1913) found that the production of bilateral ridges adventitiously or in response to changes other than seasonal was exceptionally rare. On only one occasion did he identify a 'false check'

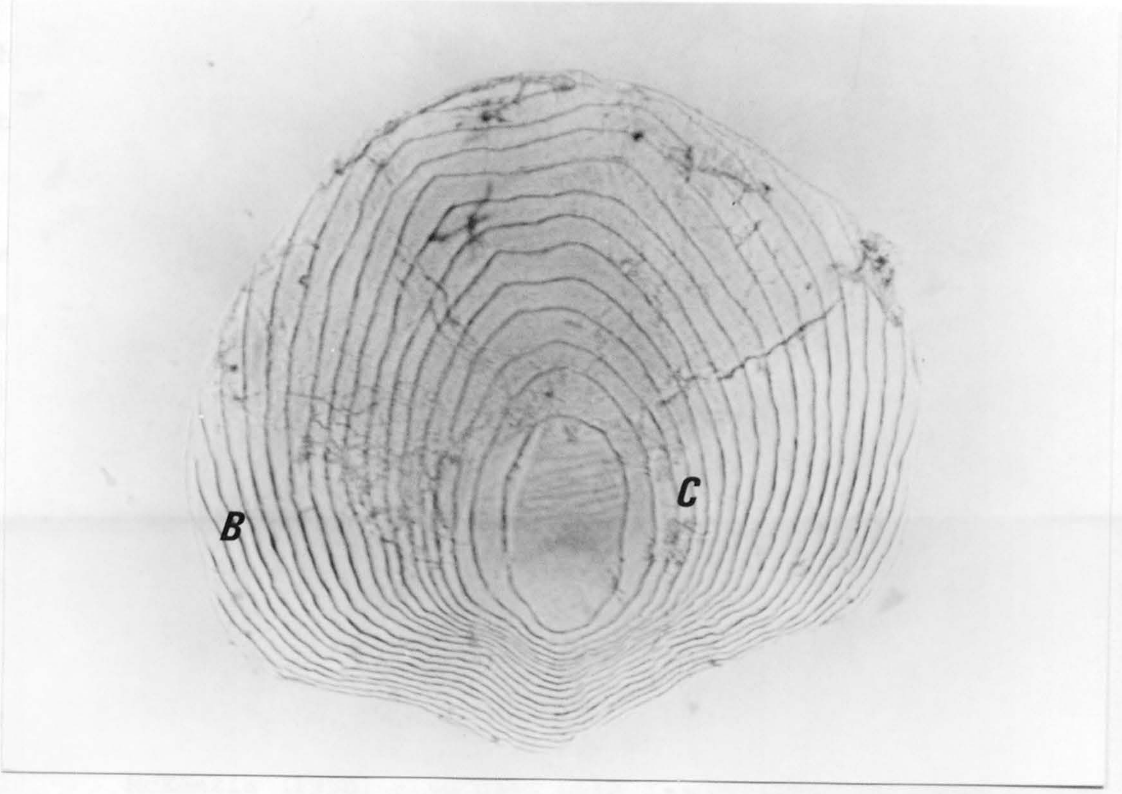


PLATE 5: The scale of a smelt approaching the end of its first year of life, showing concentric (C) and bilateral (B) circuli.

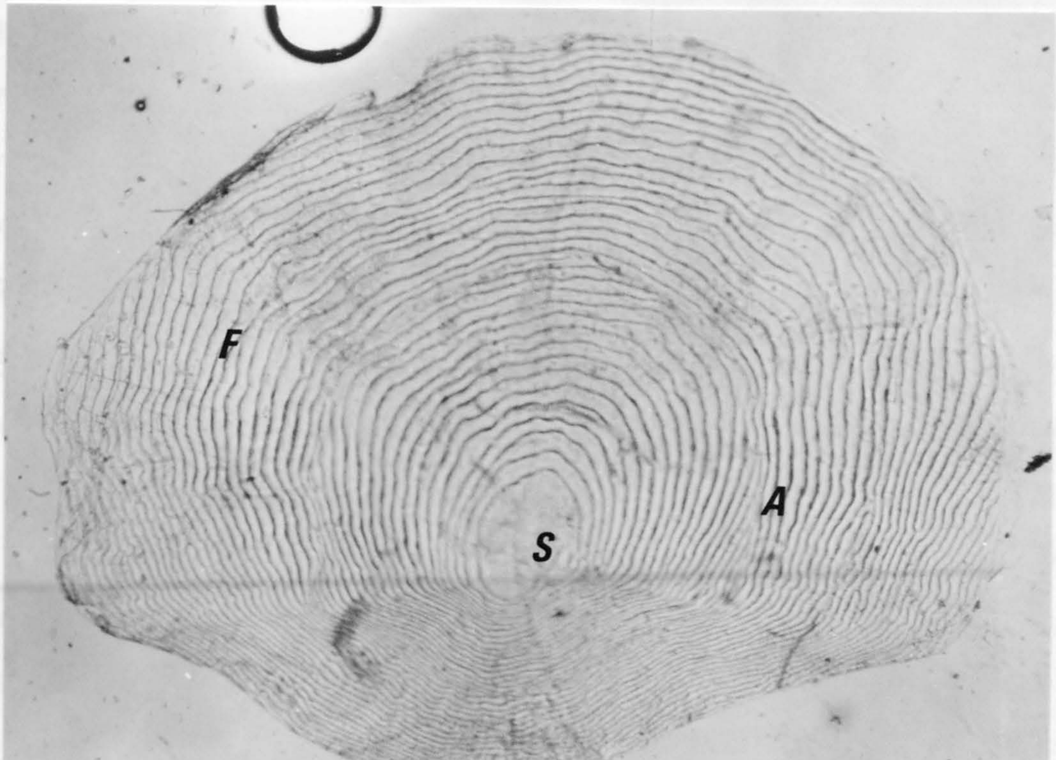


PLATE 6: The scale of a smelt approaching the end of its second year of life showing a spiral circulus (S), false check (F) and first annulus (A).

which consisted of two bilateral ridges succeeding the central ring. However, detection of false checks is facilitated by the presence of a slight scar which forms at the junction of the zones of slow and rapid growth (McKenzie, 1958; Belyanina, 1969). McKenzie (1958) termed this scar the 'shiny line' and considered that evidence provided by water temperatures, hatching times and growing seasons all substantiated the 'shiny line' as the true criterion of an annulus.

The combination of the cutting over of a series of progressively shortening bilateral circuli by concentric circuli, and the presence of a 'shiny line' provides a rationale for the separation of true and false annuli and was used to age smelt in this study.

McKenzie (1958) also used this 'shiny line' to identify the annulus on the unsculptured scales of late hatching 0+ year old fish. The age at which the smelt in this study first formed their scales could not be determined, but by the time the 0+ year old Thames smelt appeared in the screen samples (August 1981) the scales already possessed considerable sculpturing. McKenzie (1958) found that smelt in the river Miramichi formed scales two months after hatching, and the smallest smelt (37 mm) from western Lake Superior also possessed well sculptured scales (Bailey, 1964). In contrast, smelt, *Osmerus eperlanus*, from the Elbe (Ehrenbaum, 1909) and Neva (Gribb, 1946) (in Belyanina, 1969) rivers did not form scales until they were 4 months old.

Although the scales of smelt lack the absorption or abrasion of the scale edge necessary for studying the previous spawning history, the determination of the age of smelt is "a matter of extreme simplicity and certainty" (Masterman, 1913).

The scale samples, which had been mounted up according to the

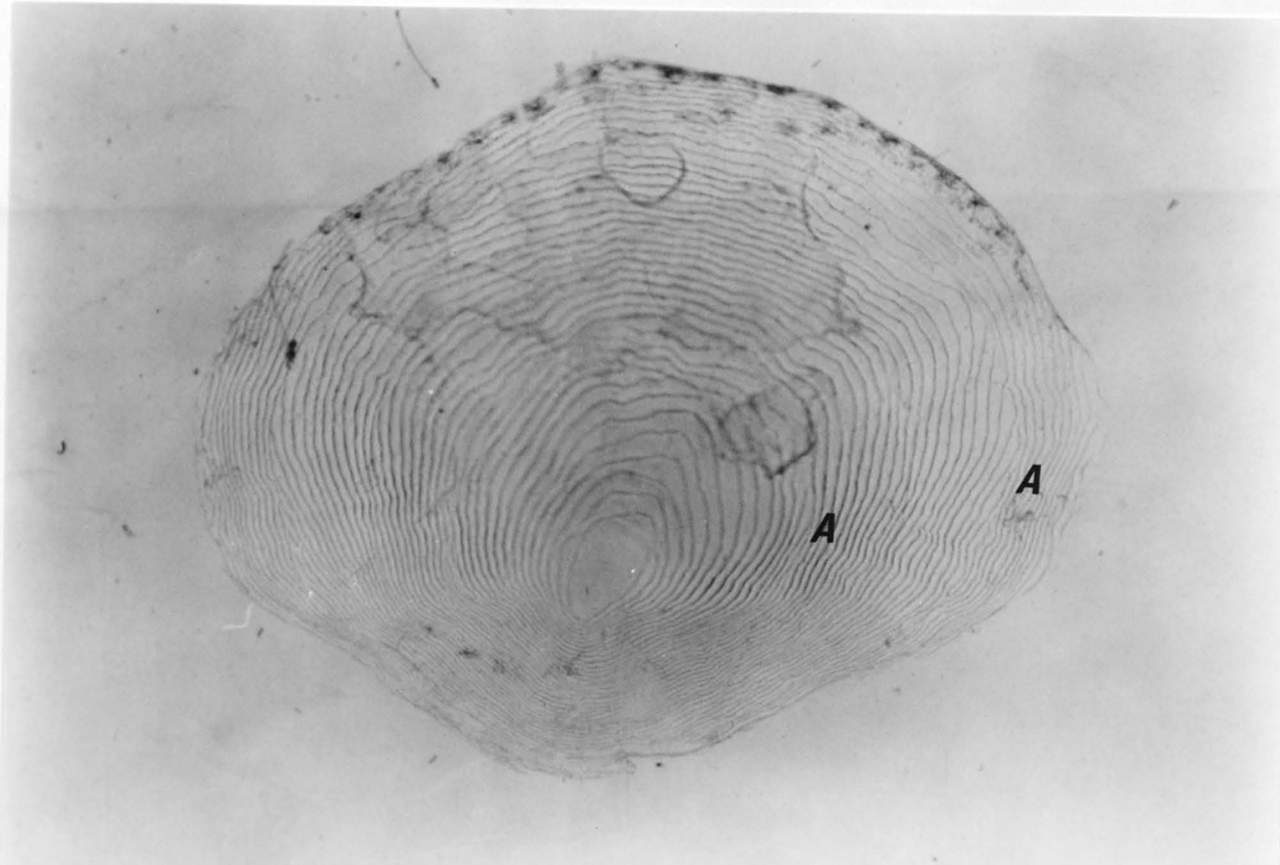


PLATE 7: The scale of a smelt in its third year of life showing the position of the first two annuli (A).

technique outlined in Chapter 2, were viewed by projecting on a Mikrops microprojector (Flatters and Garnett Limited, Manchester, England) using a magnification of X 55 and aged, without reference to the corresponding length or weight measurements, according to the criteria outlined above. The number of circuli after the last annulus, or in the case of 0+ year old fish from the centre of the scale, was recorded in order to investigate the timing of annulus formation. Scales were re-read at a later date, without reference to the original estimate, in order to reduce observer error.

4:2:2 The Determination Of Back-Calculated Length

Having aged the fish, the position of each annulus and of the outermost edge of the scale was recorded on a strip of card bearing the serial number of the fish. The edge of the card was aligned so that it passed through the centre of the scale and was inclined at an angle of approximately 70° to the horizontal.

This angle was chosen because it cut an area of the scale which was easy to read and because the lateral axis of the scale undergoes a morphometric change in older fish. In the first year of growth the scale is approximately oval in shape, but the scales of fish in succeeding years show large extensions in the lateral plane such that the antero-posterior axis is less than half the lateral axis (Masterman, 1913). Since it is desirable to establish one relationship between fish length and scale radius the lateral axis was avoided. Furthermore, only scales which had been taken from the shoulder region of the fish were used to establish the fish length/scale radius relationship and in subsequent back-calculations, since the shape of the scale varies according to its location on the fish (Masterman, 1913).

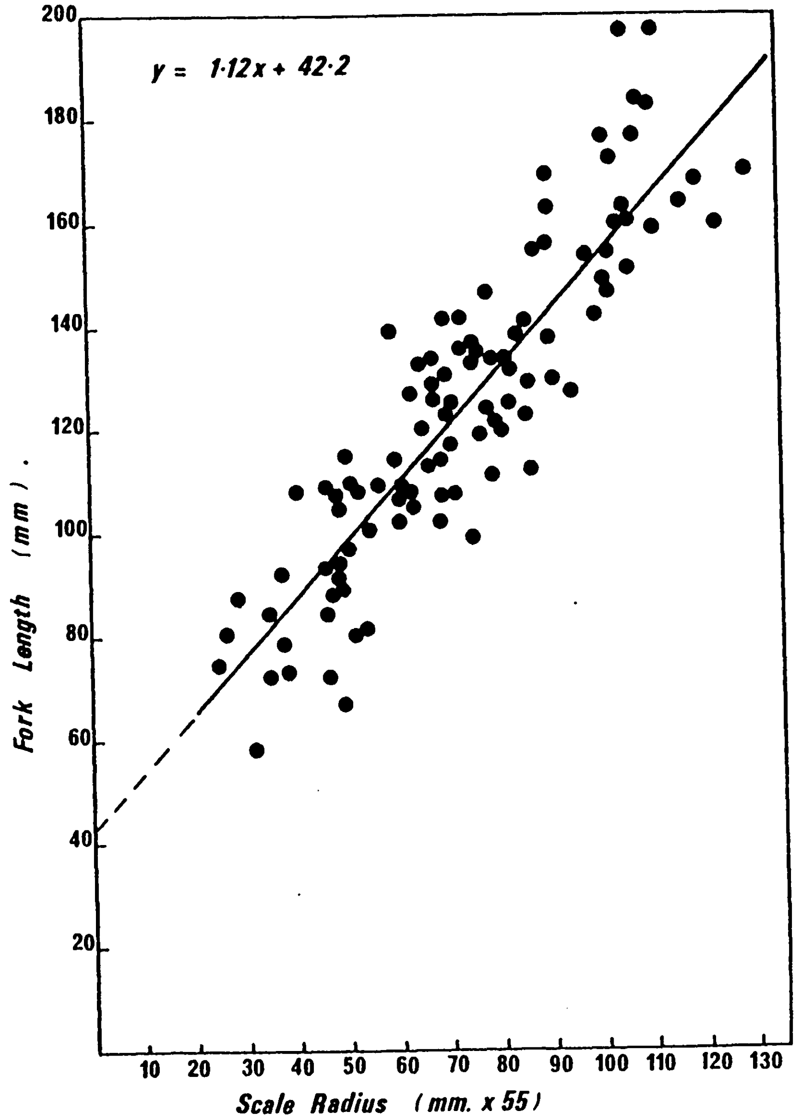


FIGURE 5: The relationship between fork length and scale radius for smelt from the river Thames (r = 0.83, p < 0.001)

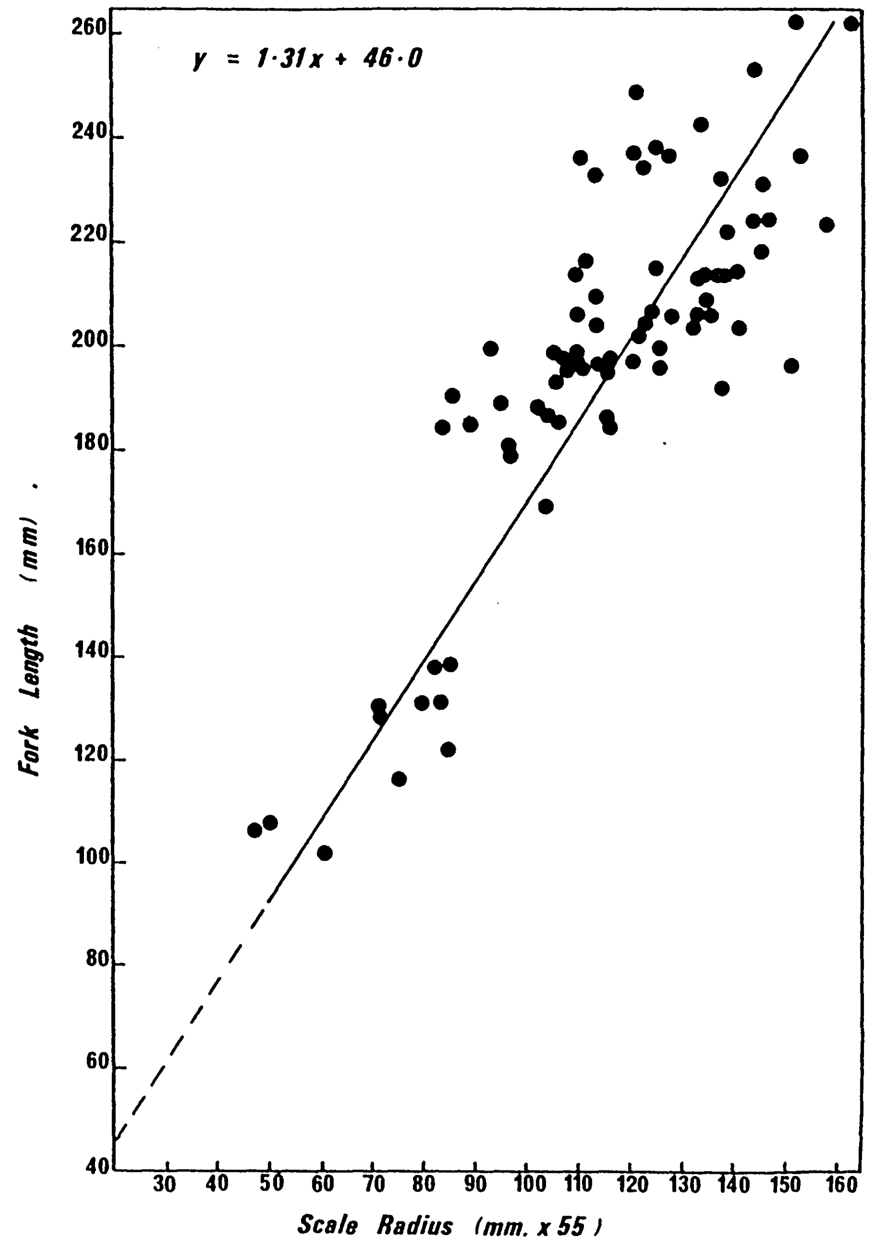


FIGURE 6: The relationship between fork length and scale radius for smelt from the river Cree (line fitted by eye).

The relationship between fish length (ordinate) and scale radius (abscissa) was then determined according to the procedure described by Bagenal and Tesch (1978) using a least squares regression. This relationship is shown in Figures 5 and 6 for the rivers Thames and Cree, respectively.

Plots of ageing structure radius (ordinate) against fish length (abscissa) have been used (eg. Fry, 1943; Le Cren, 1947) but it is preferable to compute the regression of fish length (ordinate) on ageing structure radius (abscissa) since the resulting equation will be used to estimate fish lengths from a given ageing structure radius (Whitney and Carlander, 1956; Bagenal and Tesch, 1978).

The Dahl-Lea equation, which assumes isometric growth, was rejected since the fitted regression lines did not pass through the origin. The data was also plotted on logarithmic co-ordinates but the resulting correlation coefficients ($r = 0.35$ and $r = 0.14$ for the rivers Thames and Cree respectively) indicated that a better fit was obtained using a normal plot. Whitney and Carlander (1956) doubted that the body-scale regression was ever strictly linear, and Mottley (1942) showed that the variances of scale lengths are correlated with body lengths. A logarithmic transformation eliminates this correlation (Whitney and Carlander, 1956). However, in view of the increased labours involved Whitney and Carlander (1956) concluded that in most growth studies it is sufficiently accurate to dispense with the logarithmic transformation.

The established relationship between fish length and scale radius was used to determine the length of fish at the time of the formation of previous annuli. In particular, these data were extremely useful for the river Cree since few 0+ year old fish were obtained during sampling.

4:2:3 The Validation Of Age Analysis

Bagenal and Tesch (1978) believed that errors in age determinations arise most frequently as a result of a failure to detect the first annulus, or as a result of closely spaced annuli in older fish. It has been stated in Section 4:2:1 that the first annulus was clearly detectable with all 0+ year old fish exhibiting considerable scale sculpturing at the time of capture. Subsequent annuli were found by Bailey (1964) to be easily detectable and the short-cycle nature of the smelt populations in this study undoutedly assisted ageing since very closely spaced annuli did not occur. In the longer lived (12+ years old) smelt populations of the White Sea (Belyanina, 1969) this problem may result in errors in age determinations.

Bagenal and Tesch (1978) listed five methods of validating age determinations and it was decided to use one of these methods, comparison with length frequency histograms (Peterson method), to investigate the value of length measurements as a predictor of age. This technique is most appropriate for fish with a short spawning season and rapid and uniform growth, although care must be taken to ensure that the modes belong to successive age groups and not to dominant year classes which have been separated by scarcer broods.

4:2:4 The Analysis Of Growth

In addition to back-calculated data, the growth of smelt was investigated using the length and weight measurements derived according to the procedure outlined in Chapter 2.

Within any stanza of a fish's life, weight varies as some power of length according to the equation:

$$W = aL^b$$

or $\log W = \log a + b \log L$ (i)

Ricker (1975) considered that a G.M. functional regression should be used in preference to the more usual predictive least squares method to estabish this relationship. However, the validity of the G.M. regression has not yet been generally accepted by statisticians (Bagenal and Tesch, 1978), and in this study the least squares method was adopted.

Vaznetsov (1953) (in Tesch, 1968) stated that during their development fish typically pass through several stages of growth, each of which may have its own length-weight relationship. However, Tesch (1968) pointed out that several stages are completed during embryonic and larval life so that for many species post-larval growth comprises a single stage. Changes in 'b' often occur at first maturity and with environmental changes, and changes in 'a' often occur with changes of season, with time of day and between habitats (Bagenal and Tesch, 1978).

The seasonal pattern of growth was investigated by determining the mean length and weight of each age group on a monthly or seasonal basis. This information was used to identify the period of active growth so that compensation along the age axis of the growth curves could be made to take account of the time of year when the observations were made (Williams, 1963).

Growth was also expressed in terms of the instantaneous rate of increase according to the expressions:

$$G_L = \frac{\log_e l_2 - \log_e l_1}{t_2 - t_1} \quad \text{and} \quad G_W = \frac{\log_e w_2 - \log_e w_1}{t_2 - t_1}$$

(Ricker, 1975; Bagenal and Tesch, 1978).

The parameters of the Von Bertalanffy growth model were derived using the extrapolative Ford-Walford plot of l_{t+1} against l_t (Ford, 1933; Walford, 1946) which enabled an estimate of the asymptotic length (L_∞) and the Von Bertalanffy coefficient (K) to be made. The Bertalanffy model enables a generalised description of the pattern of growth to be made, which is free from the minor variations of the original observations and which facilitates comparisons of a given species at various times and places (Dickie, 1978).

The condition of the fish was determined using Fulton's condition factor (K) defined as :

$$K = 100w/l^3$$

Previous investigations of smelt populations have adopted this index of condition (eg. Bailey, 1964; Jilek, Cassell, Peace, Garza, Riley and Siewart, 1979) which is satisfactory where growth is approximately isometric. K may also be used when growth is allometric provided that the length range of the fish is small. If the length range is large however a new factor defined as:

$$K' = 100w/l^b$$

where 'b' is derived from equation (i) should be adopted (Bagenal and Tesch, 1978). Weatherley (1972) questioned the value of the laborious readjustments made in the computation of condition factors other than K, and bearing in mind the small size range of smelt and the fact that comparisons with other studies would be facilitated, Fulton's index would appear to be the most suitable.

The condition factor was calculated on a monthly (river Thames) or seasonal (river Cree) basis using both total and somatic weight so that the influence of the sexual cycle on condition could be determined.

4:3 RESULTS

4:3:1 Length-Frequency Analysis

Length-frequency histograms are shown on a monthly basis for the river Thames in Figures 7, 8 and 9.

Prior to August 1981, the samples from the river Thames were dominated by smelt of the 1979 year class. The 1977 and 1978 year classes were poorly represented with the former being absent from samples taken later than March 1981. The 1978 year class failed to appear in samples taken later than September 1981, with a maximum of three year classes being represented after this date. The 1981 year class first appeared in the screen catches in August 1981, with the smallest fish recorded being 60 mm fork length. This year class was dominant in the samples from September 1981 - May 1982.

The length-frequency histograms for the river Cree are shown on a seasonal basis in Figure 10.

These histograms highlight the low representation of 0-group fish in the samples, possible explanations of which have already been discussed (Chapter 2). As was the case in the river Thames, a maximum of four year classes was recorded in the samples. The 1980 year class dominated the samples in each season and the 1978 year class failed to appear in the summer sample.

The data from both study sites illustrate that the establishment of dominant year classes separated by scarcer broods makes it extremely difficult to identify age groups reliably from the distribution of length-frequency modes in such small samples. Furthermore, there is considerable overlap of the length ranges of the different age groups (see Figure 11). In the river Thames, the length ranges of 0+ and 1+ year old smelt overlap almost completely although their modes are

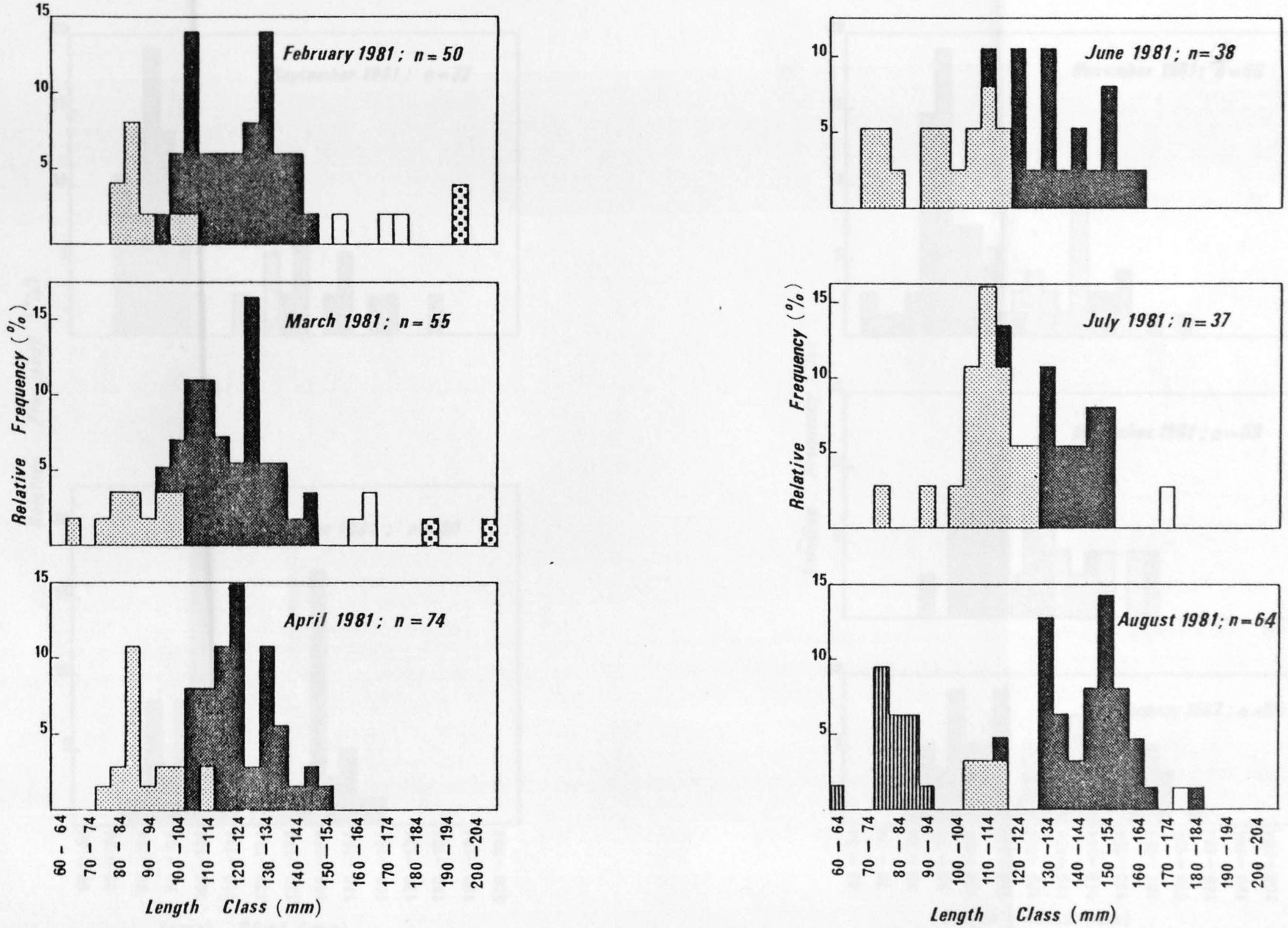


FIGURE 7: Length frequency histograms for the smelt samples from the river Thames, February 1981 - August 1981. (1977 year class; 1978 year class; 1979 year class; 1980 year class; 1981 year class).

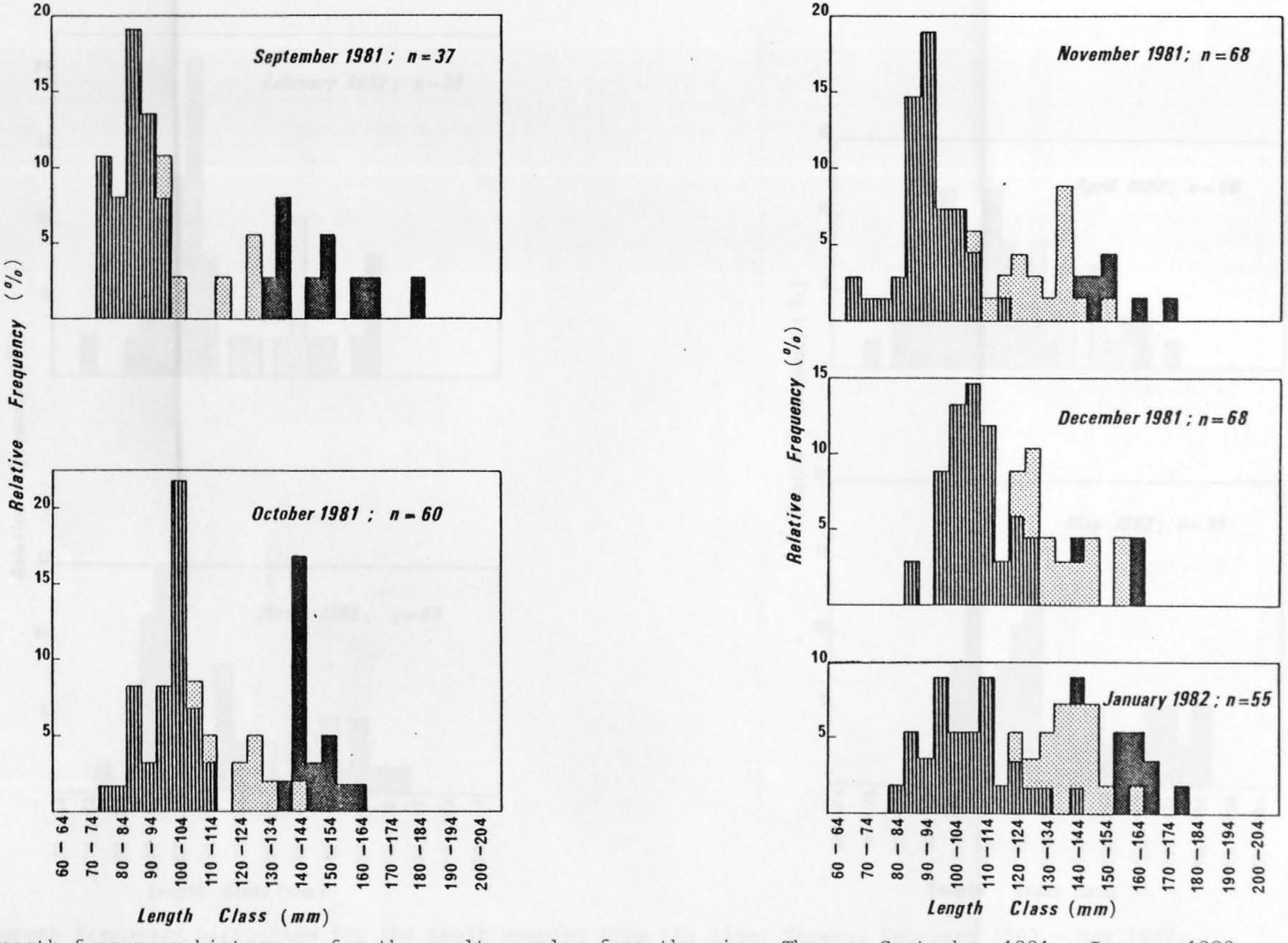


FIGURE 8: Length frequency histograms for the smelt samples from the river Thames, September 1981 - January 1982. (Legend as in Figure 7).

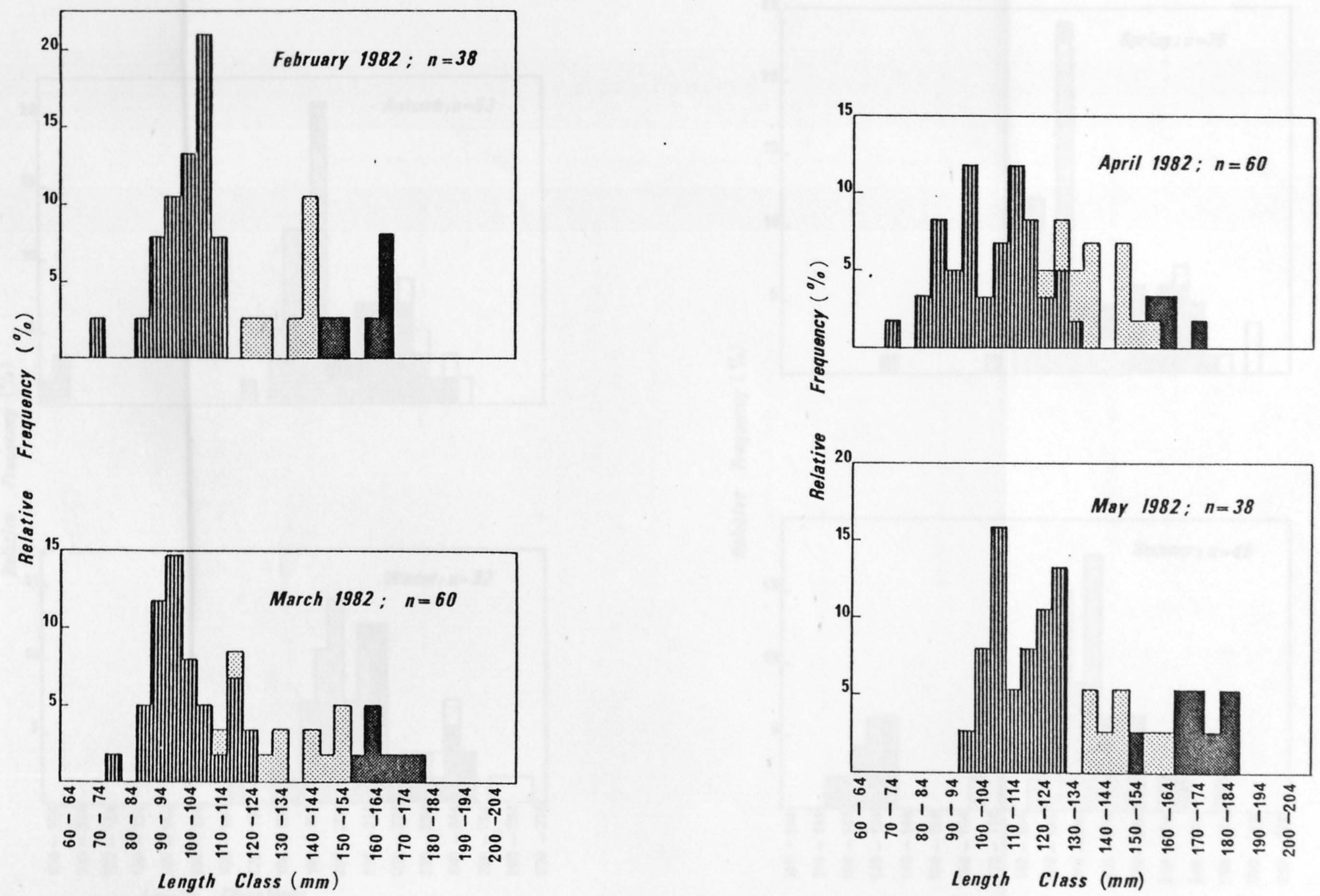


FIGURE 9: Length frequency histograms for the smelt samples from the river Thames, February 1982 - May 1982. (Legend as in Figure 7).

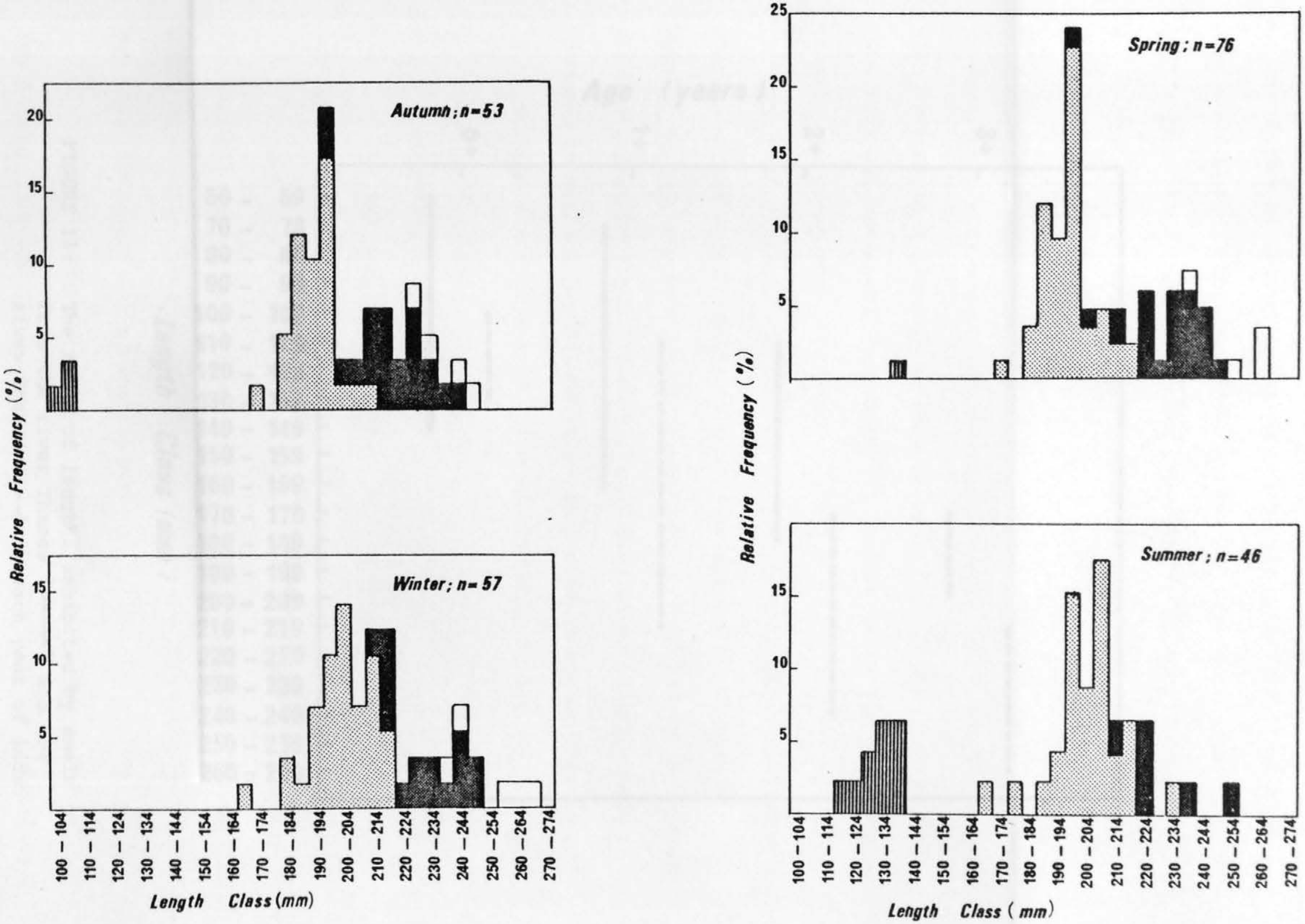


FIGURE 10: Length frequency histograms for the smelt samples from the river Cree, Autumn (November 1981) - Summer (July 1982). (1978 year class; 1979 year class; 1980 year class; 1981 year class).

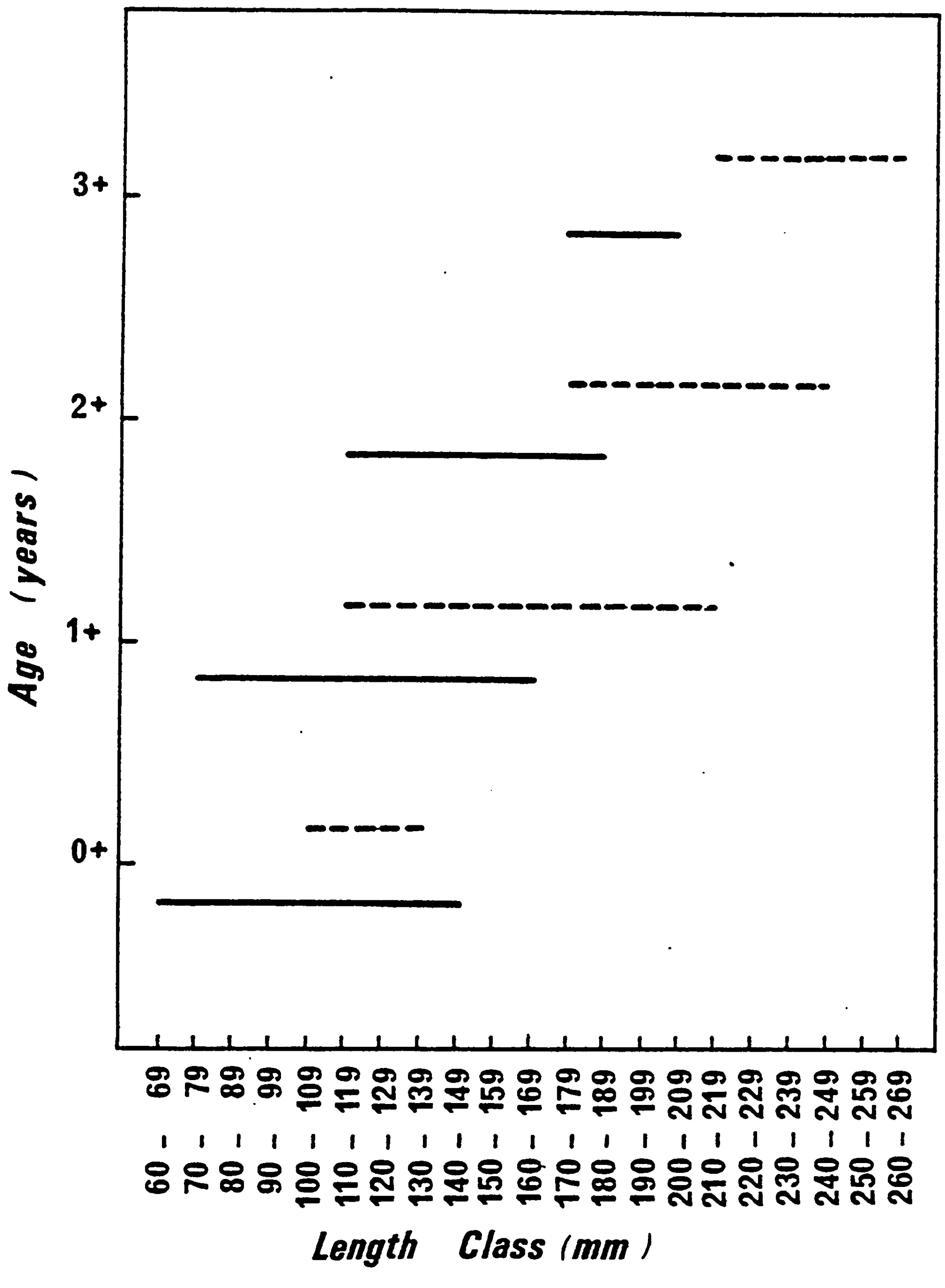


FIGURE 11: The range of lengths exhibited by smelt from the river Thames (——) and the river Cree (----) in each year of life.

separated by one 10 mm size group. It is likely that the improved growth rate of 0+ year old smelt of the 1981 year class contributed to the degree of overlap. The length ranges of 1+ and 2+ year old fish overlapped in six 10 mm size groups and the length ranges of 2+ and 3+ year old Thames smelt overlapped in two 10 mm size groups. 0+, 1+ and 2+ year old fish all occurred in the 110 - 119 mm to 140 - 149 mm size groups.

The length ranges of 1+ and 2+ year old Cree smelt overlapped in five 10 mm size groups and the length ranges of 2+ and 3+ year old fish overlapped in four 10 mm size groups. 1+, 2+ and 3+ year old fish were all present in the 210 - 219 mm size group but again the modes of each age group were separated.

Bailey (1964) and Burbidge (1969) also found considerable overlap of the length ranges of the older age groups of smelt, Osmerus mordax, but 0-group fish were usually isolated in their length frequency distribution. In this study, overlap of length ranges occurred in all age groups and it would therefore appear that length is a poor indicator of age, as also concluded by Bailey (1964).

4:3:2 Longevity

The age composition of the samples from the Thames and Cree estuaries is shown in Tables 9 and 10 respectively.

Both populations of smelt are characterised by a short-cycle life history with no fish being found to have formed a fourth annulus. Males and females were present in all age groups but marked changes in sex ratio occurred with increasing age.

In the river Thames, male smelt were numerically dominant in the 0-group fish and the sex ratio was significantly different from

AGE GROUP	SEXES COMBINED		HERMAPHRODITES		MALES		FEMALES		MALE:FEMALE	$X^2 - \frac{1}{2}$	P
	Abs.	Rel(%)	Abs.	Rel(%)	Abs.	Rel(%)	Abs.	Rel(%)			
O	353	43.9	2	0.6	216	61.2	128	36.3	1.69 :1	22.00	<0.001
I	286	35.5	12	4.2	139	48.6	129	45.1	1.01 :1	0.30	>0.5
II	155	19.2	7	4.5	71	45.8	77	49.7	0.92 :1	0.17	>0.5
III	11	1.4	-	-	3	27.3	8	72.7	0.37 :1	1.45	>0.1

TABLE 9: The age composition and the sex ratio in each age group of smelt from the river Thames.

AGE GROUP	SEXES COMBINED		MALES		FEMALES		MALE:FEMALE	$X^2 - \frac{1}{2}$	P
	Abs.	Rel(%)	Abs.	Rel(%)	Abs.	Rel(%)			
O	4	16	1	25.0	2	50.0	0.5 :1	0	-
I	131	52.4	85	64.9	46	35.1	1.84:1	11.61	<0.001
II	90	36.0	53	58.9	37	41.1	1.43:1	2.50	>0.05
III	25	10.0	13	52.0	12	48.0	1.08:1	0	-

TABLE 10: The age composition and the sex ratio in each age group of smelt from the river Cree.

unity (X^2 = 22.00, $p < 0.001$). Male fish were also numerically dominant in I-group smelt from the river Cree and the sex ratio was also significantly different from unity (X^2 = 11.61, $p < 0.001$). At both study sites however, the numerical dominance of the males became less in the older age groups, particularly in the river Thames where females outnumbered males by approximately 3:1 in the oldest age group. The sex ratios were not however significantly different from unity.

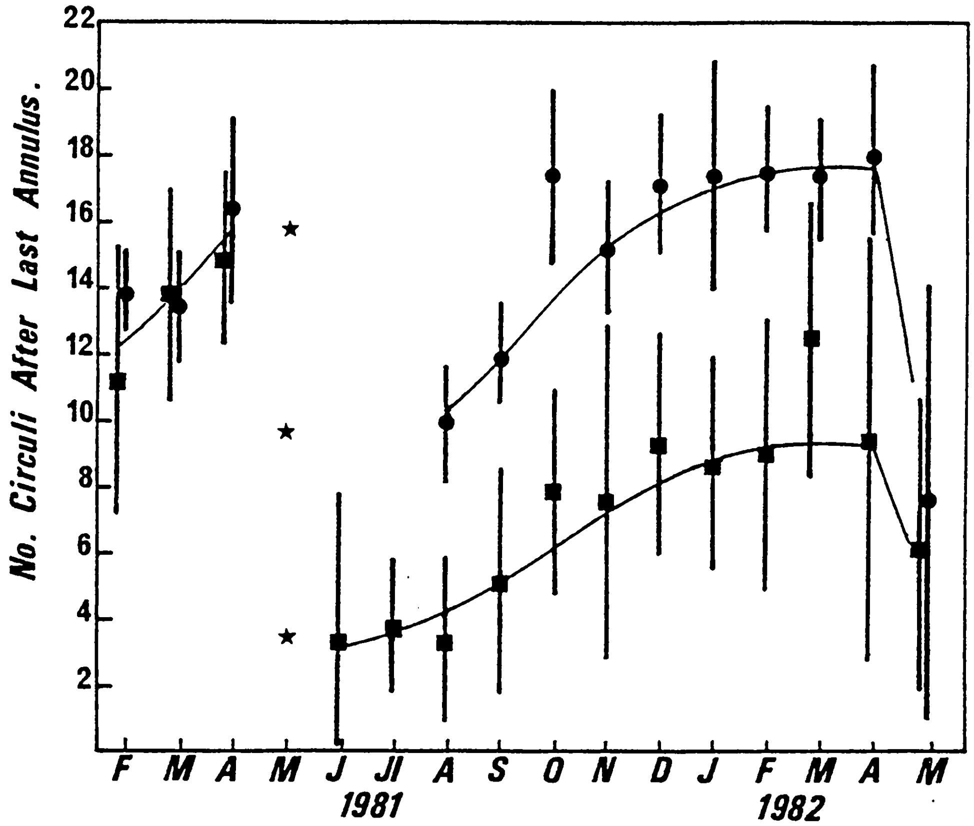
4:3:3 Time Of Annulus Formation

The number of circuli outside the last annulus, or encircling the scale origin in the case of 0-group fish, is shown in Figure 12 for the river Thames. There was a marked reduction in the number of 'current year' circuli between the April 1981 (1% of fish had formed an annulus) and June 1981 (88% of fish had formed an annulus) samples. By the time the July 1981 samples were collected all fish had formed annuli and in some cases up to 8 circuli had been laid down outside the last annulus. A similar pattern was evident in 1982 with a marked decrease in the number of circuli between April 1982 (15% of fish had formed an annulus) and May 1982 (65% of fish had formed an annulus).

On the basis of these results, 1st June was designated the theoretical birth date of Thames smelt, although it should be noted that annulus formation commenced as early as April and was not completed until July. 0-group Thames smelt will actually be approximately 14 months old on their first theoretical birthday.

The number of circuli outside the last annulus is shown in Figure 13 for smelt from the river Cree. It can be seen that a marked reduction in the number of 'current year' circuli occurred between the spring and summer sampling dates. By the time the summer samples

FIGURE 12: Seasonal variation in the number of circuli outside the last annulus or scale origin for Thames smelt (● 0+ years old; ■ >0+ years old). Vertical bars represent ± 1 standard deviation (S.D.).



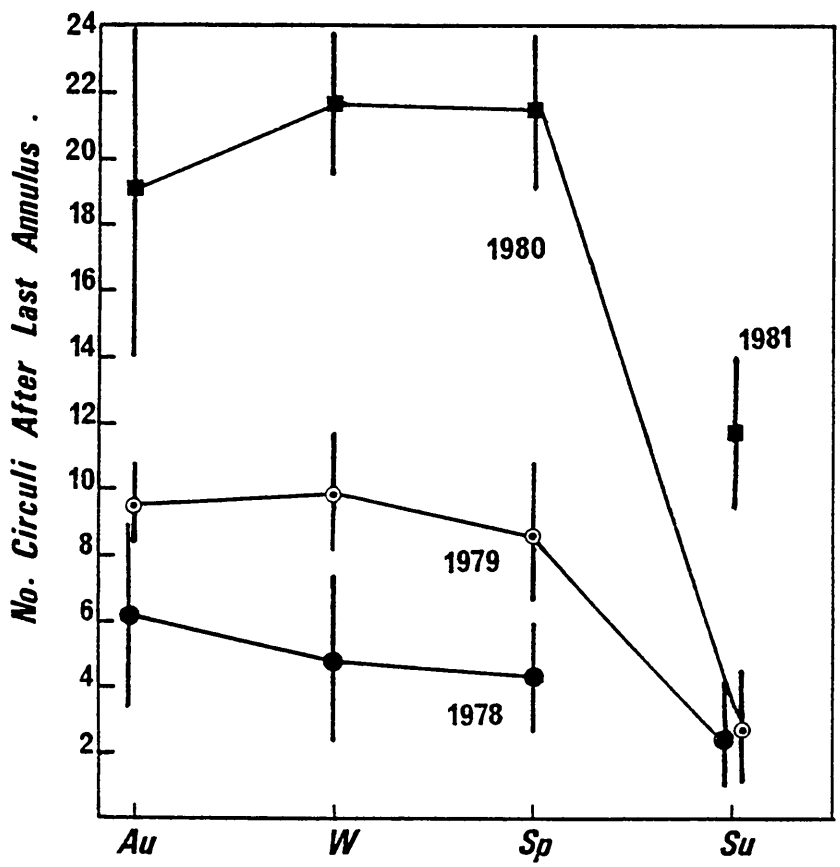


FIGURE 13: Seasonal variation in the number of circuli outside the last annulus for Cree smelt (■ 1+ years old; ⊙ 2+ years old; ● 3+ years old). Vertical bars represent ± 1 S.D.).

★ no samples.

were collected all fish had formed their annuli and in some cases up to 13 circuli had been laid down outside the annulus. Annulus formation must also therefore occur in early summer in the river Cree.

McKenzie (1958) found that smelt, Osmerus mordax, in the river Miramichi formed their annulus in spring but did not specify in which month. In western Lake Superior, Bailey (1964) identified annual variation in the time of annulus formation, but during the two years of her study annuli were formed between early July and mid-August. Murawski and Cole (1978) indicated that annulus formation generally occurred after the spawning season but again failed to be more specific.

4:3:4 The Seasonal Pattern Of Growth In Length And Weight

The seasonal pattern of growth in length and weight is shown in Figures 14 and 15 for the river Thames, and Figures 16 and 17 for the river Cree.

In the river Thames, insignificant growth occurred in all age groups between February - April 1981. Unfortunately, no samples were collected in May 1981 but between April and June insignificant growth in both length and weight occurred in fish of the 1980 year class. Fish of the 1979 year class however, showed significant growth in both length and weight between April and June ($t_L = 4.14$, $t_W = 4.14$, $p < 0.001$). The main growth period of Thames smelt occurred between June and December. During this period significant increases in both length and weight occurred in I($t_L = 8.32$, $t_W = 10.14$, $p < 0.001$) and II($t_L = 2.87$, $p < 0.01$; $t_W = 2.74$, $p < 0.05$) group fish. The seasonal pattern of growth in 0-group fish was followed from August - December and during this period a significant

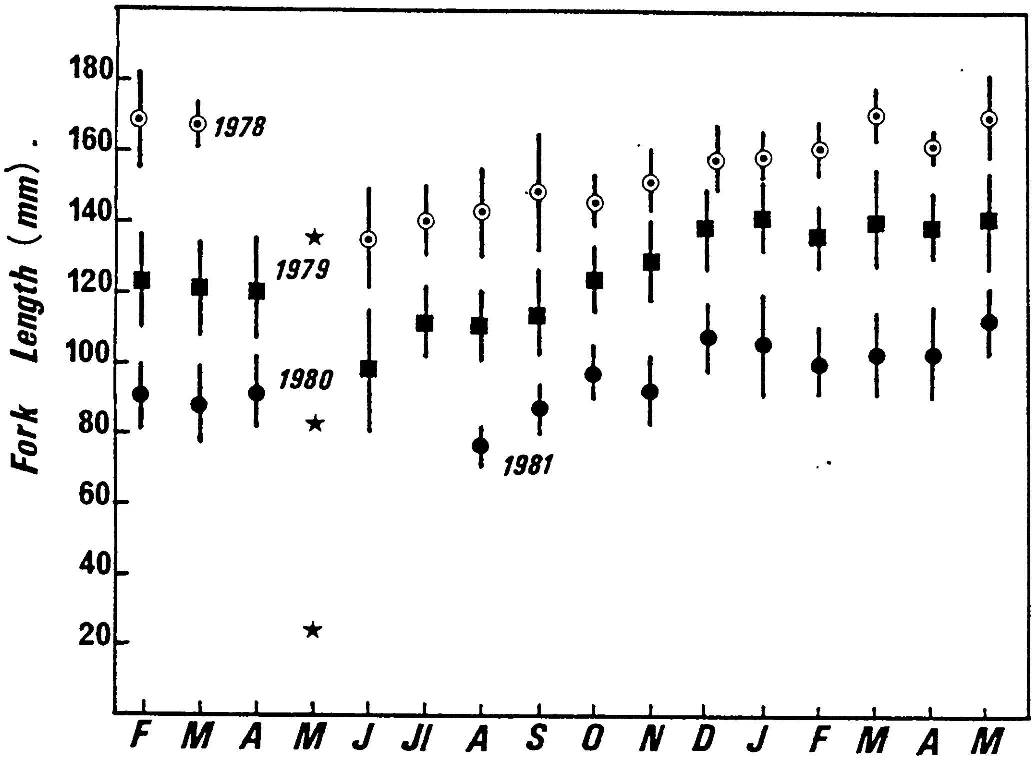


FIGURE 14: The seasonal pattern of growth in length of Thames smelt. (● 0+ years old; ■ 1+ years old; ⊙ 2+ years old. Vertical bars represent ± 1 standard deviation).

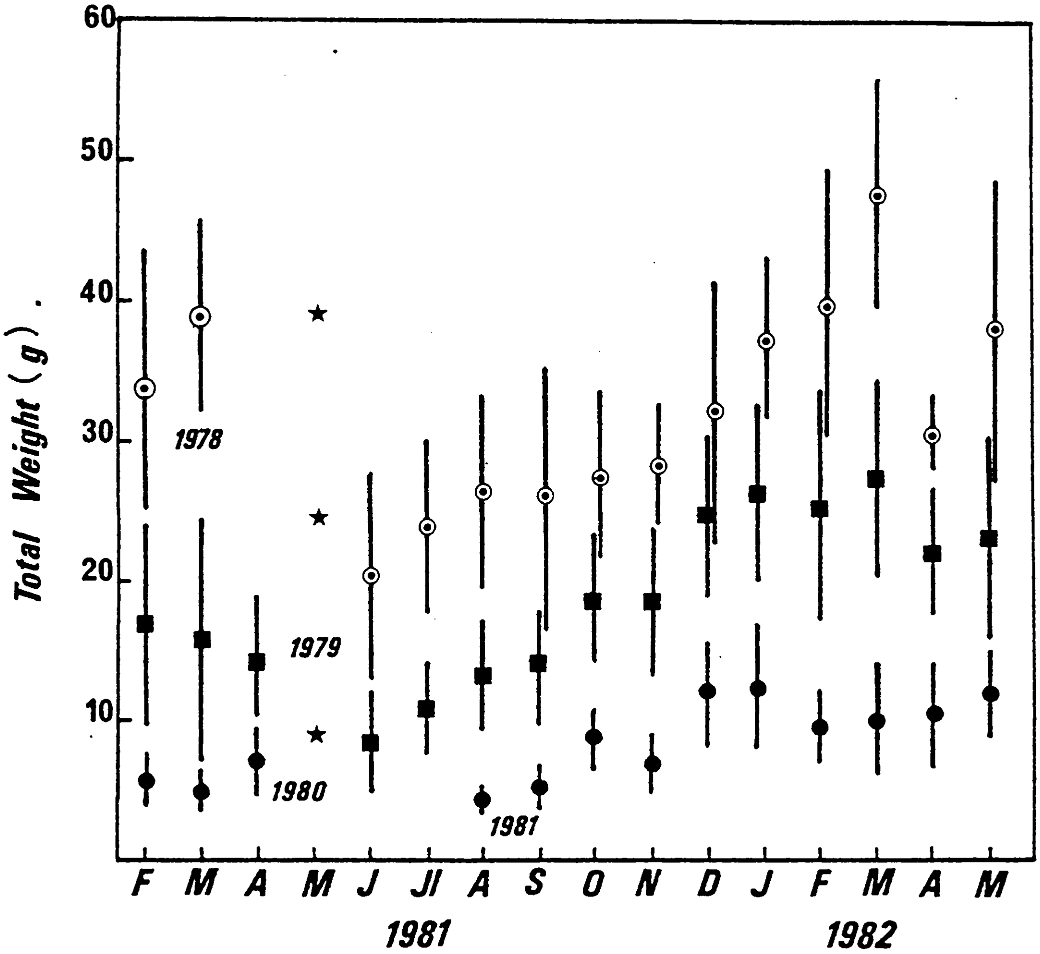


FIGURE 15: The seasonal pattern of growth in weight of Thames smelt. (Legend as in Figure 14).

★ no samples.

increase occurred in both length and weight ($t_L = 12.05$, $t_W = 11.68$, $p < 0.001$).

The period from December 1981 to March 1982 was characterised by insignificant ($p > 0.05$) changes in both length and weight in 0 and I group fish, but II group fish showed a significant weight gain ($t = 2.87$, $p < 0.05$). In the period between the March - April 1982 sampling dates, significant weight losses occurred in both I($t = 2.37$, $p < 0.05$) and II($t = 4.42$, $p = 0.001$) group fish, presumably as a result of the shedding of gonadal products. No such weight loss was evident in 0-group fish.

With the exception of 0-group fish which showed a significant increase in length ($t = 2.55$, $p < 0.05$) growth in both length and weight was insignificant in all age groups between April - May 1982.

Lillelund (1961) considered that the length of the growing season differed for different age groups, and 0-group fish have generally been found to begin growth earlier than older individuals (Lillelund, 1961; Bailey, 1964). Belyanina (1969) believed the difference in growing season length to be related to the spawning activities of older fish which delayed the onset of somatic growth. While there was evidence that 0-group fish recommenced growth earlier than older individuals in 1982, no such trend was apparent in 1981.

In the river Cree, the period between the autumn and winter sampling dates was characterised by significant increases in both length and weight in I($t_L = 3.48$, $t_W = 9.25$, $p < 0.001$) and II($t_L = 2.75$, $p < 0.01$; $t_W = 4.21$, $p < 0.001$) group fish. III group fish showed insignificant growth in length and weight during this

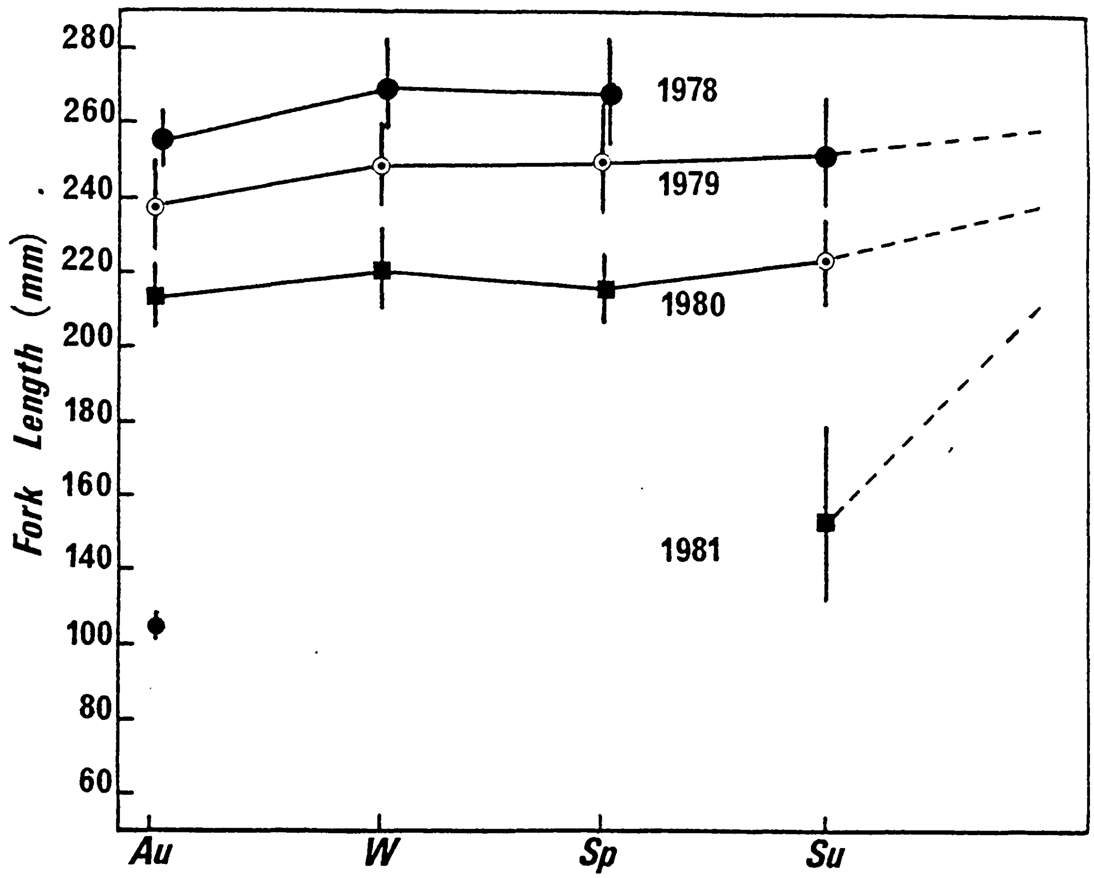


FIGURE 16: The seasonal pattern of growth in length of Cree smelt. (● 0+ years old; ■ 1+ years old; ⊙ 2+ years old; ● 3+ years old. Vertical bars represent ± 1 S.D.).

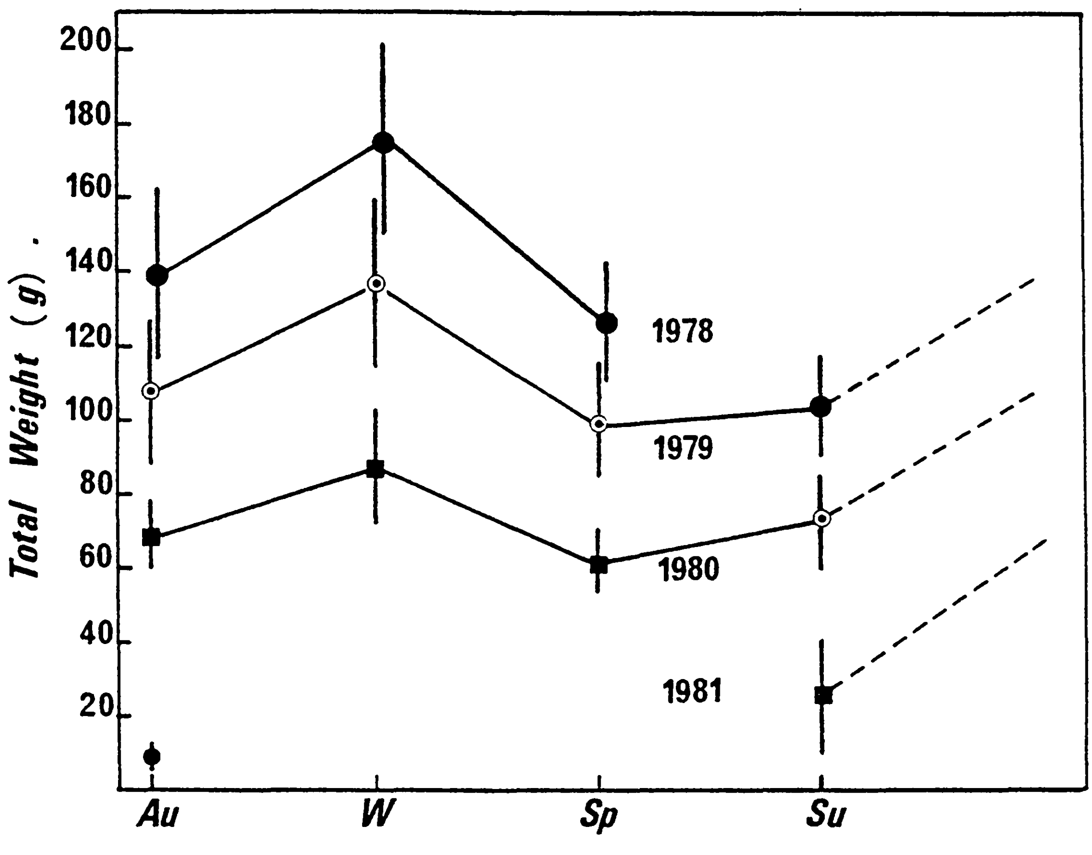


FIGURE 17: The seasonal pattern of growth in weight of Cree smelt. (Legend as in Figure 16).

period.

In the period between the winter and spring sampling dates there were insignificant changes in the length of all age groups, but significant reductions in weight in I($t = 9.36$, $p < 0.001$), II($t = 6.18$, $p < 0.001$) and III($t = 2.71$, $p < 0.05$) group fish. Again, this weight loss was presumably as a result of spawning activities.

At some stage between the collection of the spring and summer samples, growth in both length and weight was resumed although only to a significant extent in fish of the 1980 year class ($t_L = 3.74$, $t_W = 4.52$, $p < 0.001$).

The seasonal pattern of growth in both the Thames and the Cree supports the findings of Bailey (1964) who showed that continued growth of smelt, Osmerus mordax, was possible after the fall.

4:3:5 Growth In Length

The data presented in section 4:3:4 were used to construct growth curves for the length of fish at the approximate time of annulus formation.

In the river Thames, with minor exceptions, the length of fish taken between January - June samples should approximate to the length at annulus formation since in most age groups insignificant growth occurred in this period. Figure 18 presents data for the growth of Thames smelt both in terms of length at capture (annulus formation in 1981 and 1982) and back-calculated length.

There was very close agreement between length at capture (annulus formation 1981) and back-calculated data, with no significant differences being evident. There was also close agreement

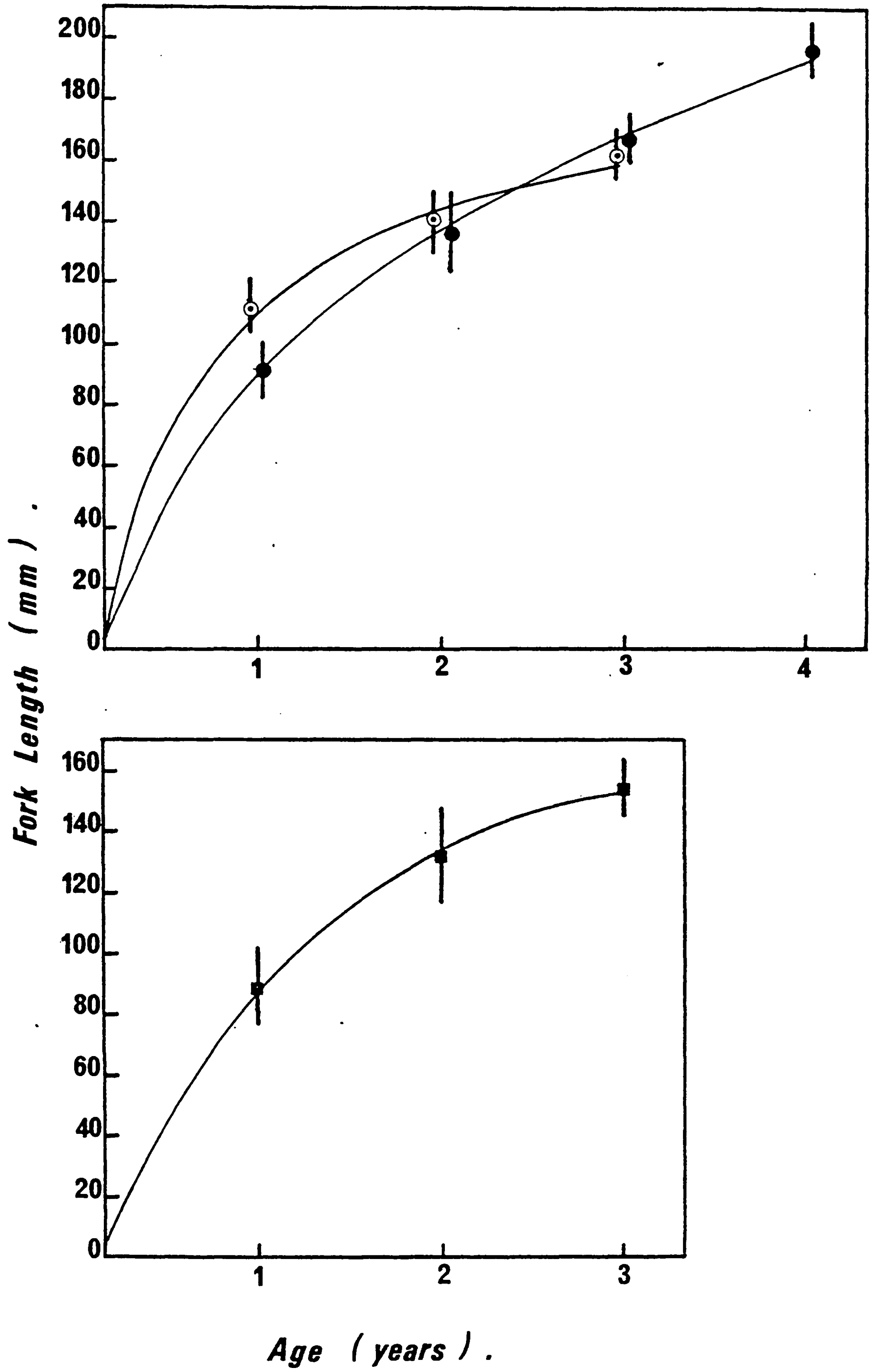


FIGURE 18: The growth in length of smelt from the river Thames. (● length at capture [annulus formation 1981]; ⊙ length at capture [annulus formation 1982]; ■ back-calculated length. Vertical bars represent ± 1 S.D.).

	AGE (YEARS)			
	0+	1+	2+	3+
FEMALES	101.1 ± 2.3 (68.0 - 141.0)	125.9 ± 3.1 (70.0 - 159.0)	151.3 ± 3.5 (111.0 - 184.0)	181.9 ± 15.2 (147.0 - 206.0)
MALES	97.7 ± 1.8 (60.0 - 133.0)	124.0 ± 2.7 (72.0 - 168.0)	144.9 ± 3.5 (113.0 - 183.0)	172.3 (159.0 - 184.0)
HERMAPHRODITES	113.0	126.0 ± 10.0 (101.0 - 151.0)	150.1 ± 8.8 (137.0 - 168.0)	-
SEXES COMBINED	98.9 ± 1.4 (60.0 - 141.0)	124.5 ± 2.0 (70.0 - 168.0)	148.3 ± 2.4 (111.0 - 184.0)	179.3 ± 11.4 (147.0 - 206.0)

TABLE 11: The mean fork length (mm) of smelt of different ages from the river Thames (± 95% confidence limits (if n ≥ 5) and range of values in parentheses).

	AGE (YEARS)			
	0+	1+	2+	3+
FEMALES	104.0 (103.0 - 105.0)	190.9 ± 6.9 (125.0 - 217.0)	221.5 ± 6.2 (185.0 - 260.0)	251.9 ± 7.2 (234.0 - 266.0)
MALES	106.0	191.3 ± 4.0 (116.0 - 218.0)	216.6 ± 3.9 (179.0 - 246.0)	232.8 ± 7.0 (214.0 - 258.0)
SEXES COMBINED	111.0 (101.0 - 130.0)	191.2 ± 3.5 (116.0 - 218.0)	218.7 ± 3.3 (179.0 - 260.0)	242.0 ± 6.2 (214.0 - 266.0)

TABLE 12: The mean fork length (mm) of smelt of different ages from the river Cree (± 95% confidence limits (if n ≥ 5) and range of values in parentheses).

between the length at capture (annulus formation 1982) and back-calculated data although the length at capture was significantly greater than back-calculated length at the end of the first year of life ($t = 9.74$, $p < 0.001$). This difference was a result of the much improved first year growth by 0-group fish of the 1981 year class, with the mean length of 0+ year old fish being significantly greater in April 1982 than in April 1981 ($t = 3.31$, $p < 0.01$).

Table 11 shows that the mean length of female Thames smelt was greater than that for males in all age groups, and that the difference in mean length of the sexes became greater in the older age groups. However, the differences between the mean length of the sexes were only significant for 0+ ($t = 2.33$, $p < 0.05$) and 2+ ($t = 2.55$, $p < 0.05$) year old fish. Similarly, the differences in length between the sexes were generally insignificant in terms of the length at annulus formation. Thus, one year old female smelt were significantly longer than males at the time of capture (annulus formation 1981) ($t = 2.33$, $p < 0.05$) and according to back-calculated data ($t = 3.10$, $p < 0.01$). All other comparisons between the length of the sexes at the time of annulus formation revealed insignificant differences and the data in the growth curves were therefore pooled.

The mean length of hermaphroditic Thames smelt in each age group is also shown in Table 11. The mean length of 0+ year old hermaphrodites was significantly greater than both females ($t = 10.14$, $p < 0.001$) and males ($t = 16.66$, $p < 0.001$) of the same age. The probable reason for this difference is that only mature 0-group hermaphrodites could be identified, and as shown in Chapter 5 the attainment of sexual maturity in 0-group fish is size related. In the older age groups the differences in length between hermaphrodites

	AGE (YEARS)										
	0		I		II		III		IV	L∞	K
1977			100		146		154		-	165	0.91
G_L		2.81		0.38		0.05		-			
1978			96		137		154		-	169	0.81
G_L		2.77		0.36		0.17		-			
1979			85		132		-		-	-	-
G_L		2.65		0.44		-		-			
1980			101		-		-		-	-	-
G_L		2.82		-		-		-			
1981*			91		135		168		196	235	0.45
G_L		2.72		0.39		0.22		0.15			
1982*			112		140		162		-	174	1.07
G_L		2.92		0.22		0.15		-			
CV(%)			9.5		3.9		4.3				

TABLE 13: The growth in length, instantaneous growth in length and Von Bertalanffy parameters for successive year classes of Thames smelt.

CV = coefficient of variation.

* Length at capture (time of annulus formation).

	AGE (YEARS)										
	0		I		II		III		IV	L∞	K
1976			117		199		229		-	288	0.53
G_L		2.97		0.53		0.14		-			
1977			116		182		237		-	343	0.39
G_L		2.96		0.45		0.26		-			
1978			120		194		223		-	272	0.59
G_L		2.99		0.48		0.14		-			
1979			114		189		217		-	266	0.56
G_L		2.94		0.50		0.14		-			
1980			118		200		-		-	-	-
G_L		2.98		0.53		-		-			
1981			110		-		-		-	-	-
G_L		2.91		-		-		-			
1982*			130		196		230		251	275	0.62
G_L		3.07		0.41		0.16		0.09			
CV(%)			5.3		3.5		3.3				

TABLE 14: The growth in length, instantaneous growth in length and Von Bertalanffy parameters for successive year classes of Cree smelt.

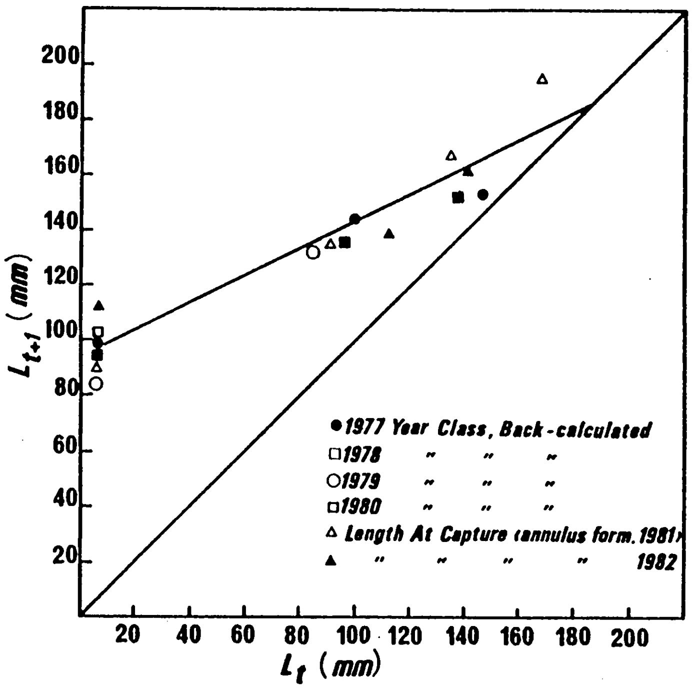


FIGURE 19: Ford-Walford plot for smelt from the river Thames. An asymptotic length of 187 mm has been derived.

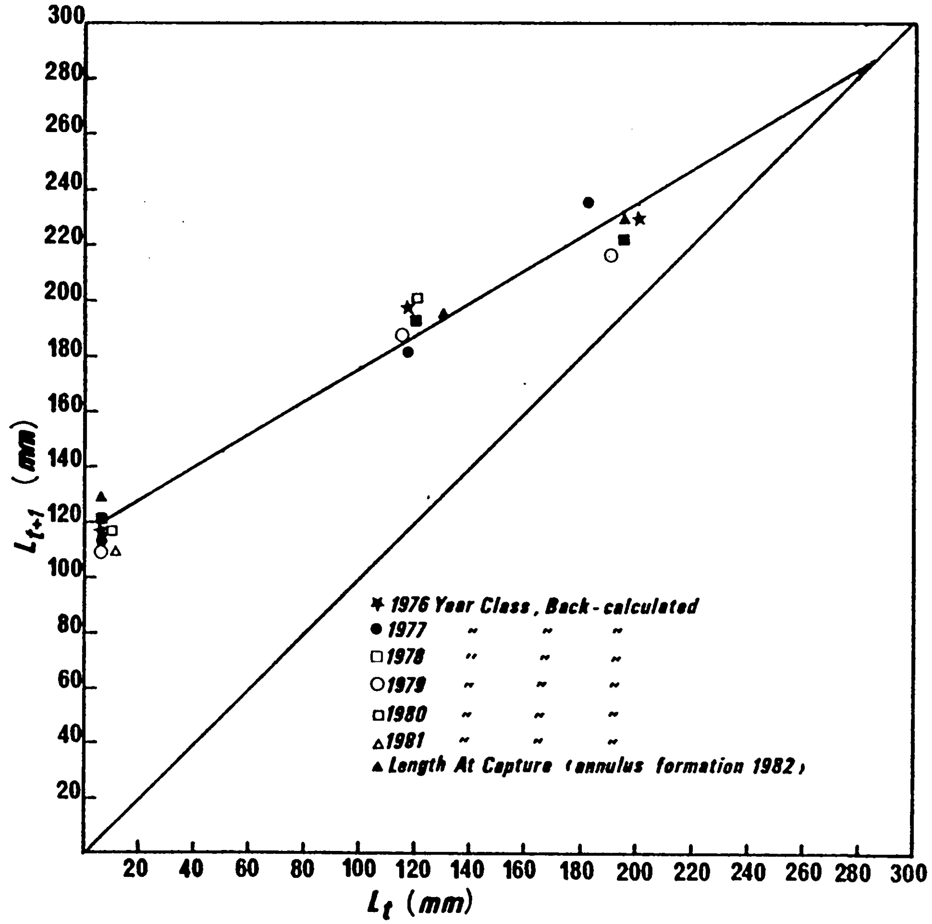


FIGURE 20: Ford-Walford plot for smelt from the river Cree. An asymptotic length of 283 mm has been derived.

and gonochorists of both sexes were insignificant, although the growth more closely resembled that of females.

Table 13 presents data for the growth in length of the 1977 - 1980 year classes of Thames smelt. It can be seen that first year growth was the most variable. Instantaneous growth in length of Thames smelt was highest in the first year of life, declined rapidly in the second year and continued to decline with age.

An estimate of the asymptotic length ($L\infty$) was obtained by the extrapolative Ford-Walford procedure shown in Figure 19. A value of 187 mm was obtained for $L\infty$ and the Von Bertalanffy coefficient (K), calculated as $-\log_e$ slope, was calculated as 0.70. The asymptotic length of 187 mm compared with a maximum observed length of 206 mm. $L\infty$ and K values for each year class are shown in Table 12. $L\infty$ values ranged from 165 - 235 mm and the corresponding K values ranged from 0.45 - 1.07.

The data presented in section 4:3:4 showed that in the river Cree the majority of the seasonal growth occurred prior to the winter sampling date, and that insignificant growth in length occurred between winter and spring. Although the infrequent sampling programme prevented accurate identification of the time of annulus formation, length at capture in winter and spring, with the minor exceptions referred to in section 4:3:4, should approximate to the length at annulus formation.

The growth in length of Cree smelt in terms of both length at capture (annulus formation 1982) and back-calculated length is shown in Figure 21. It can be seen that there was close agreement between the length at capture (annulus formation 1982) and back-

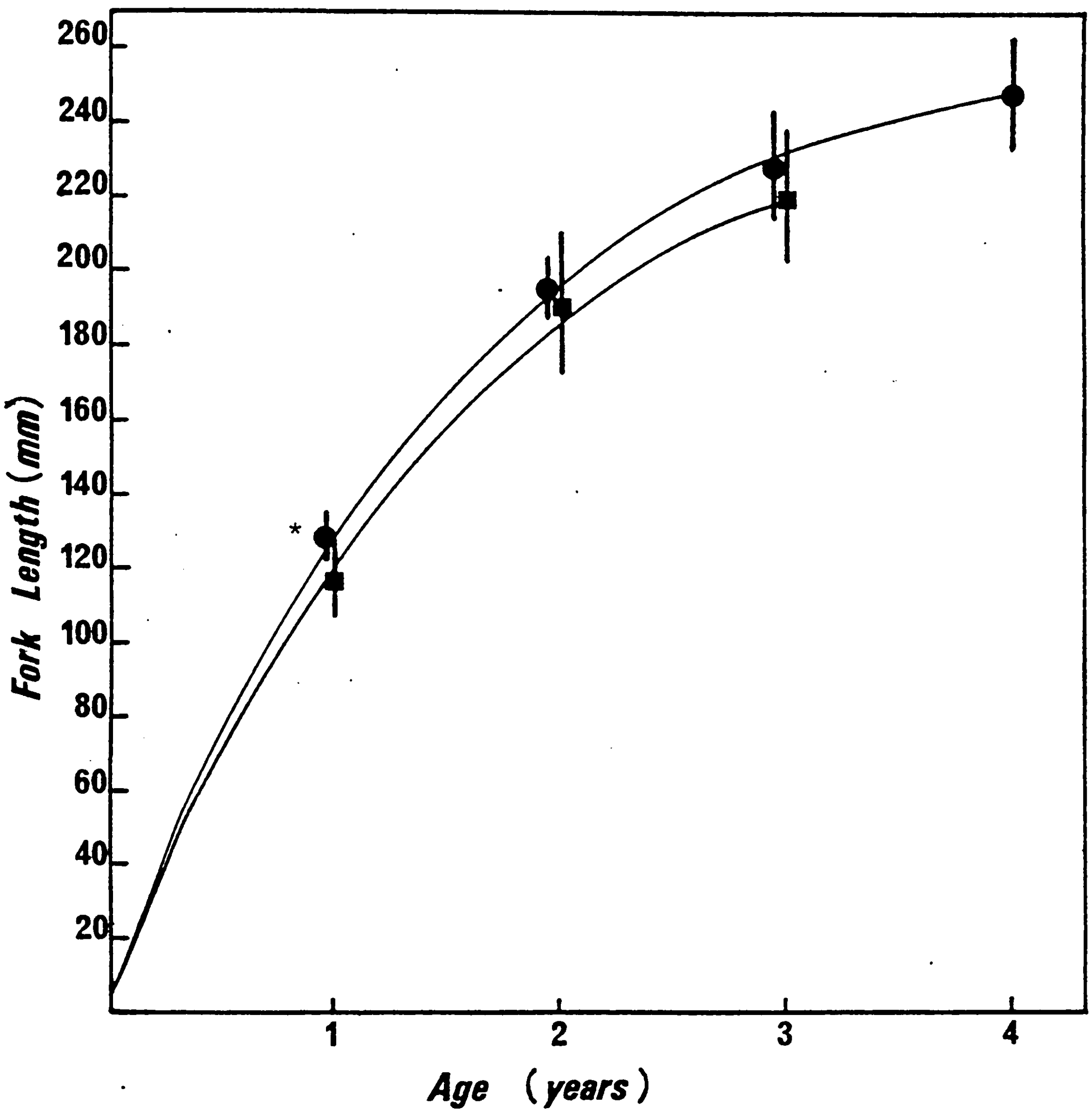


FIGURE 21: The growth in length of smelt from the river Cree. (● length at capture [annulus formation 1982]; ■ back-calculated length. Vertical bars represent ± 1 S.D.).

* mean length of 1+ year old fish taken just after formation of their first annulus in July [see text].

calculated length, although the length of one year old fish at the time of capture (annulus formation 1982) was significantly higher ($t = 5.39$, $p < 0.001$) than the corresponding back-calculated data. This difference was probably a result of using the mean length of the 1981 year class from the July 1982 samples. These fish had actually formed their first annulus and probably commenced second year growth. The possibility that the gill net was selecting for the largest 0+ year old fish cannot however be excluded.

Table 12 shows that the mean length of 1+ year old males was slightly greater than the mean length of females of an equivalent age. In the older age groups however the mean length of females was greater than that for males although the only significant difference between the sexes occurred in fish of 3+ years old ($t = 4.12$, $p < 0.001$). It seems probable that the increased mortality of the older male smelt implied from Table 10 is size selective resulting in an increased difference in mean length between the sexes with age. Comparison of the length of male and female Cree smelt at the time of annulus formation also revealed that females in the oldest age groups were significantly longer than males of the same age. Thus, the oldest females were significantly longer in terms of length at capture (annulus formation 1982) ($t = 2.37$, $p < 0.05$, age = 4) and according to back-calculated length ($t = 2.20$, $p < 0.05$, age = 3).

Table 14 presents data for the growth in length of the 1976 - 1981 year classes and it can be seen that growth in length is subject to less annual variation in the Cree than in the Thames. As was the case in the Thames, the greatest instantaneous growth in length occurred in the first year of life with a rapid decline in the second year and subsequent decline with age.

An asymptotic length ($L\infty$) of 283 mm has been derived from the Ford-Walford plot shown in Figure 20, and the corresponding Von Bertalanffy coefficient (K) was calculated as 0.52. The value of $L\infty$ compared with a maximum observed length of 278 mm. $L\infty$ and K values for each year class are shown in Table 14. $L\infty$ values ranged from 266 - 343 mm and K ranged from 0.39 - 0.62.

The only other investigation of the growth of smelt, Osmerus spp., that included estimates of $L\infty$ and K was the study of rainbow smelt, Osmerus mordax, in the Parker river, Massachusetts by Murawski and Cole (1978). These authors found that $L\infty$ ranged from 249.10 - 260.14 mm and K ranged from 0.517 - 0.745, and they concluded that the estimates of K were in the range of values characteristic of fast growing fishes. The data from this study shows that K tends to be inversely related to $L\infty$ as also reported by Nash (1982).

Comparison between the mean length of Thames and Cree smelt in each age group showed that Cree smelt exhibited much greater growth than Thames smelt after the first year of life. Thus, the difference in length between 0+ year old Thames and Cree smelt was insignificant, but 1+ ($t = 32.68$, $p < 0.001$), 2+ ($t = 34.14$, $p < 0.001$) and 3+ ($t = 11.07$, $p < 0.001$) year old Cree smelt were significantly longer than Thames smelt of the same age.

4:3:6 Growth In Weight

The seasonal pattern of growth in weight discussed in Section 4:3:4 was used to construct growth curves using both total and somatic weight at the approximate time of annulus formation.

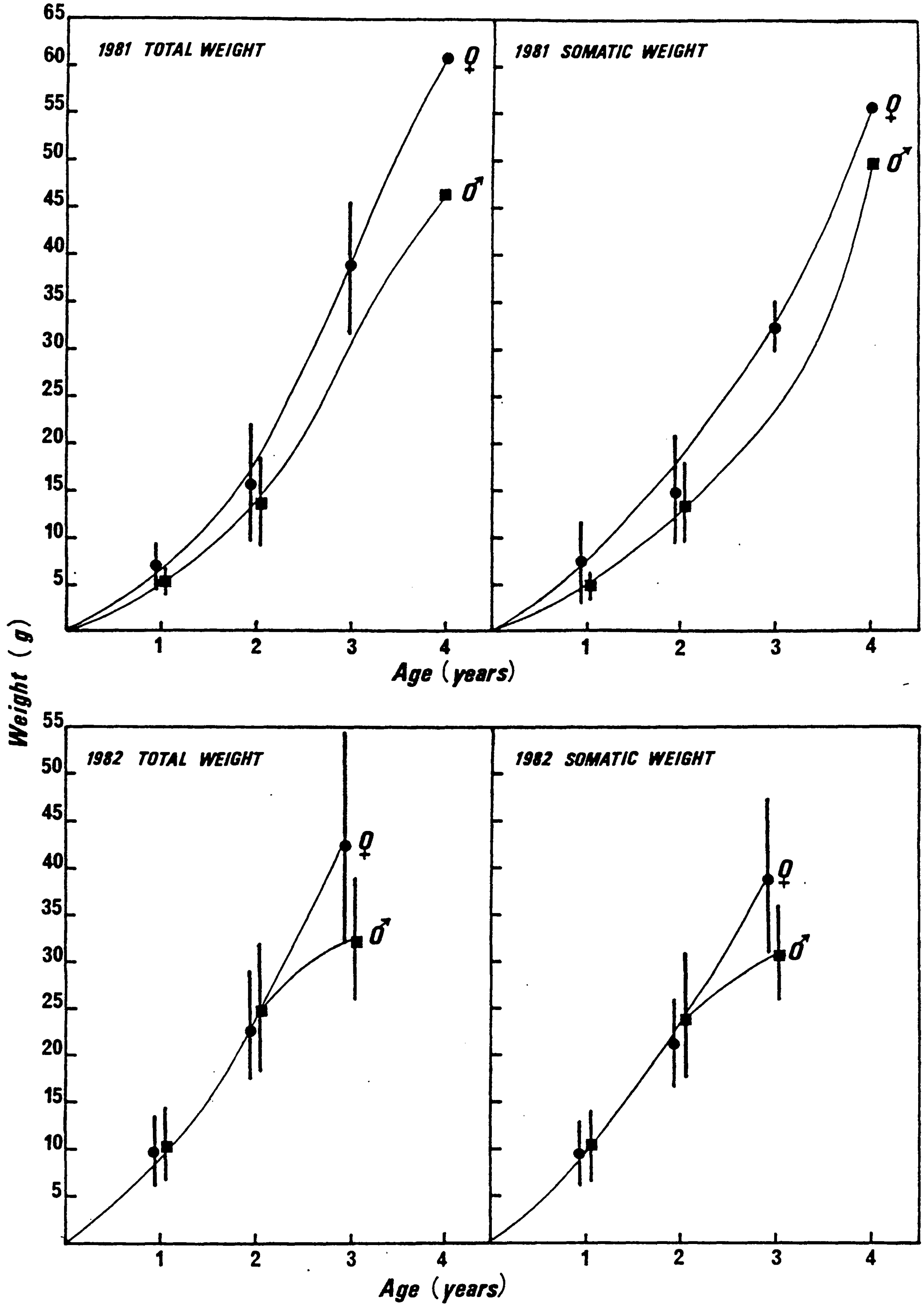


FIGURE 22: Growth in weight of Thames smelt according to weight at capture [time of annulus formation] in 1981 (top) and 1982 (bottom). (● female; ■ male. Vertical bars represent ± 1 S.D.).

	AGE (YEARS) 0+	1+	2+	3+
FEMALES	9.87 ± 0.74 (3.4 - 21.5)	17.90 ± 1.36 (4.1 - 40.1)	30.24 ± 2.26 (12.2 - 58.7)	53.00 ± 13.59 (29.5 - 77.2)
MALES	8.82 ± 0.51 (1.8 - 22.4)	16.76 ± 1.20 (4.0 - 39.6)	26.90 ± 2.10 (10.2 - 50.4)	39.73 (32.4 - 46.4)
HERMAPHRODITES	14.10 (13.0 - 15.2)	17.47 ± 4.32 (5.6 - 27.0)	28.26 ± 7.82 (19.0 - 42.0)	-
SEXES COMBINED	9.21 ± 0.42 (1.8 - 22.4)	17.13 ± 0.88 (4.0 - 40.1)	28.62 ± 1.49 (10.2 - 58.7)	49.38 ± 10.34 (29.5 - 77.2)

TABLE 15: The mean total weight (g) of smelt of different ages from the river Thames (± 95% confidence limits (if n ≥ 5) and range of values in parentheses).

	AGE (YEARS) 0+	1+	2+	3+
FEMALES	9.35 (9.3 - 9.4)	66.91 ± 7.56 (17.6 - 120.0)	101.60 ± 10.77 (54.4 - 189.8)	149.28 ± 27.17 (103.4 - 255.2)
MALES	9.40	66.92 ± 3.83 (11.9 - 107.6)	98.46 ± 6.57 (56.0 - 150.5)	120.87 - 15.16 (85.5 - 168.0)
SEXES COMBINED	11.55 (9.3 - 18.1)	66.92 ± 3.52 (11.9 - 120.0)	99.75 ± 5.68 (54.4 - 189.8)	134.51 ± 15.33 (85.5 - 255.2)

TABLE 16: The mean total weight (g) of smelt of different ages from the river Cree (± 95% confidence limits (if n ≥ 5) and range of values in parentheses).

The growth in weight of Thames smelt is shown in Figure 22. It can be seen both from Figure 22 and Table 15 that females were heavier than males in all age groups and that the differences in weight between the sexes became more marked with age. However, as was the case with growth in length, significant differences between the mean weight of the sexes were only evident amongst 0+ ($t = 2.35$, $p < 0.05$) and 2+ ($t = 2.16$, $p < 0.05$) year old fish. Instantaneous growth in weight is shown for weight at capture (time of annulus formation) data in Table 17 and it can be seen that as was the case with length, the greatest instantaneous growth in weight occurred in the first year of life. However, it should be noted that the greatest annual weight increment occurred during the third year of life.

The mean weight of hermaphrodites in each age group showed similar trends to those discussed for length. Only amongst O-group fish were the differences in weight between hermaphrodites and either males or females significant. Thus, hermaphroditic O-group smelt were significantly heavier than both males ($t=3.93, p<0.001$) and females ($t=3.11, p<0.01$).

The growth in weight of Cree smelt is shown in Figure 23. As was the case in the Thames, the difference in mean weight of the sexes became greater with age although the difference was never significant (Table 16). The highest instantaneous growth in weight of Cree smelt occurred in the first year of life (Table 18).

Comparisons between the mean weight of Thames and Cree smelt in each age group showed that the difference in weight between the study sites was insignificant for 0+ year old fish. However, 1+ ($t = 26.93$, $p < 0.001$), 2+ ($t = 23.75$, $p < 0.001$) and 3+ ($t = 9.67$, $p < 0.01$) year old Cree smelt were significantly heavier than Thames

		AGE (YEARS)								
		0		I		II		III		IV
1981*	FEMALE			6.93		15.77		38.73		61.00
	GW		11.90		0.82		0.90		0.45	
	MALE			5.66		13.81		-		46.40
	GW		11.70		0.89		-		-	
1982*	FEMALE			9.91		23.28		43.24		-
	GW		12.26		0.85		0.62		-	
	MALE			10.44		25.11		32.33		-
	GW		12.31		0.88		0.25		-	

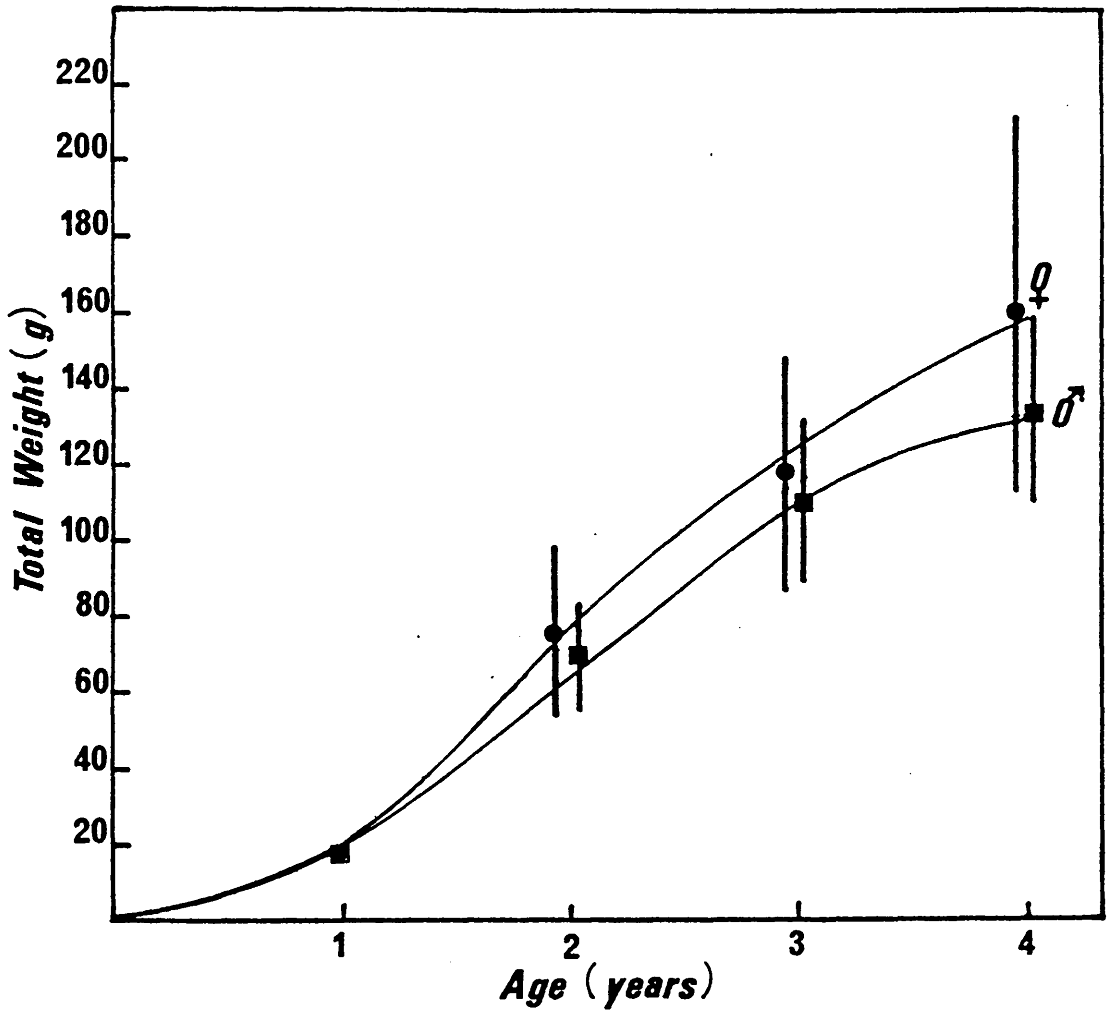
TABLE 17: The instantaneous growth in (total) weight*1 (g) of smelt from the river Thames.

		AGE (YEARS)								
		0		I		II		III		IV
1982*	FEMALE					75.90		117.66		161.98
	GW		12.86	18.10	1.43		0.44		0.32	
	MALE					69.97		110.57		134.87
	GW				1.35		0.46		0.20	

TABLE 18: The instantaneous growth in total weight*1 of smelt from the river Cree.

* weight at capture [time of annulus formation]

*1 A mean hatching weight of 0.047 mg was derived from weight measurements on newly hatched prolarvae from the egg incubation experiment.



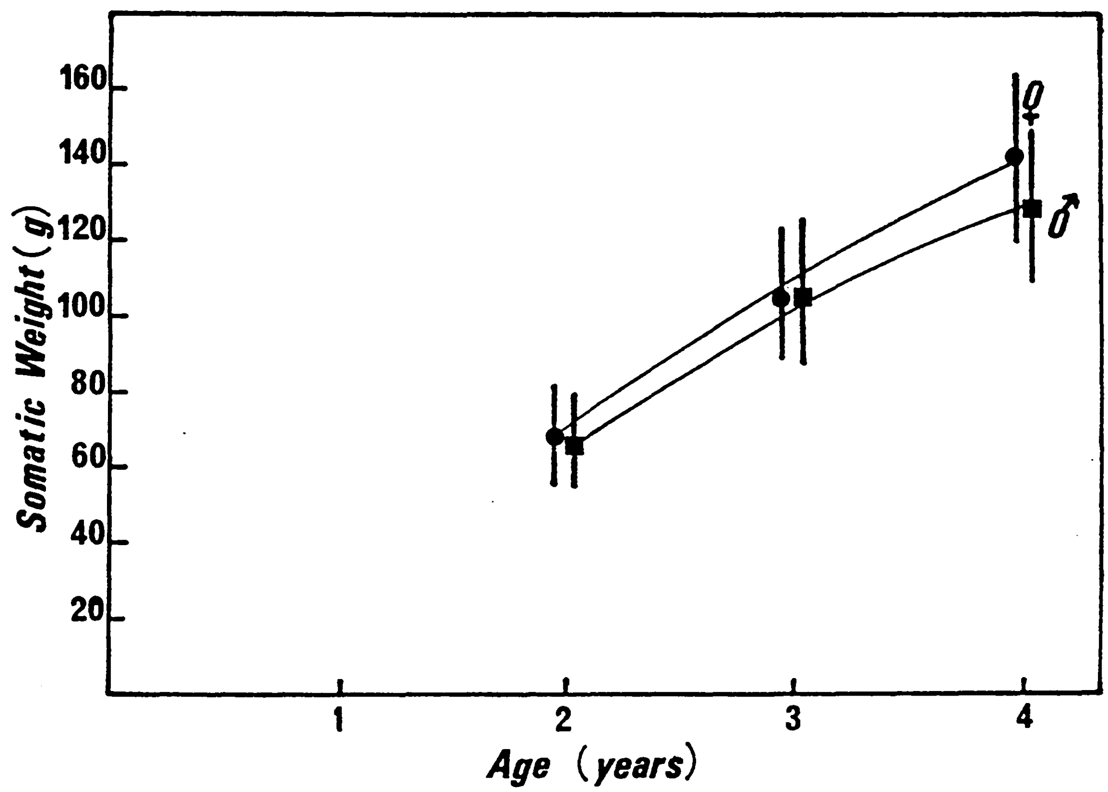


FIGURE 23: Growth in total weight (top) and somatic weight (bottom) of Cree smelt according to length at capture [time of annulus formation 1982] data. (●female; ■male. Vertical bars represent ± 1 S.D.).

		REGRESSION PARAMETERS a	b	r	STANDARD ERROR (x2)	DIFFERENCE FROM 3
FEBRUARY	Female	-2.339	3.205	0.97	0.144	*
	Male	-2.173	3.096	0.98	0.091	*
MARCH	Female	-2.577	3.404	0.97	0.144	*
	Male	-1.980	2.845	0.96	0.161	ns
APRIL	Female	-1.833	2.751	0.91	0.182	*
	Male	-1.639	2.569	0.95	0.117	*
JUNE	Female	-1.531	2.488	0.97	0.155	*
	Male	-1.757	2.695	0.96	0.129	*
JULY	Female	-2.421	3.311	0.92	0.180	*
	Male	-2.244	3.116	0.99	0.119	ns
AUGUST	Female	-1.795	2.778	0.98	0.114	*
	Male	-1.821	2.805	0.99	0.107	*
SEPTEMBER	Female	-2.002	2.930	0.99	0.123	ns
	Male	-1.787	2.693	0.98	0.105	*
OCTOBER	Female	-1.823	2.779	0.96	0.140	*
	Male	-2.083	3.039	0.98	0.110	ns
NOVEMBER	Female	-1.862	2.802	0.99	0.086	*
	Male	-1.938	2.872	0.98	0.095	*
DECEMBER	Female	-2.163	3.115	0.98	0.090	*
	Male	-1.858	2.833	0.97	0.106	*
JANUARY	Female	-1.672	2.659	0.74	0.440	ns
	Male	-1.955	2.941	0.99	0.094	ns
FEBRUARY	Female	-2.112	3.062	0.98	0.122	ns
	Male	-2.250	3.217	0.97	0.139	*
MARCH	Female	-2.205	3.156	0.99	0.097	*
	Male	-2.152	3.096	0.99	0.083	*
APRIL	Female	-1.606	2.566	0.97	0.115	*
	Male	-1.634	2.596	0.99	0.071	*
MAY	Female	-1.626	2.580	0.94	0.152	*
	Male	-1.887	2.806	0.98	0.099	*
TOTAL	Female	-1.937	2.877	0.94	0.188	ns
	Male	-1.926	2.867	0.97	0.129	*
0+	Female	-1.874	2.819	0.82	0.235	ns
	Male	-1.938	2.887	0.95	0.110	*
1+	Female	-2.001	2.928	0.91	0.171	ns
	Male	-2.186	3.091	0.93	0.142	ns
2+	Female	-1.810	2.776	0.89	0.130	*
	Male	-2.101	3.026	0.89	0.144	ns
3+	Female	-1.839	2.817	0.91	0.124	*
	Male	-1.443	2.458	0.99	-	*

* = significant difference

ns = non-significant difference

TABLE 19: Regression parameters for the least squares regressions of weight on length (logarithmic scales) for smelt from the river Thames on a monthly basis and for each age of fish.

		REGRESSION PARAMETERS a	b	r	STANDARD ERROR (x2)	DIFFERENCE FROM 3
AUTUMN	Female	-2.429	3.328	0.99	0.069	*
	Male	-2.383	3.287	0.99	0.062	*
WINTER	Female	-5.530	5.604	0.43	0.494	*
	Male	-1.960	2.981	0.98	0.023	ns
SPRING	Female	-2.000	2.923	0.96	0.038	*
	Male	-2.021	2.959	0.96	0.029	*
SUMMER	Female	-1.876	2.848	0.99	0.025	*
	Male	-2.050	2.991	0.99	0.043	ns
TOTAL	Female	-2.146	3.063	0.76	0.411	ns
	Male	-2.276	3.188	0.97	0.097	*
0+	Female	-	-	-	-	-
	Male	-	-	-	-	-
1+	Female	-1.729	2.723	0.49	0.581	ns
	Male	-2.210	3.136	0.95	0.098	*
2+	Female	-1.988	2.957	0.80	0.165	ns
	Male	-2.431	3.305	0.88	0.104	*
3+	Female	-1.919	2.912	0.53	0.078	*
	Male	-3.277	3.916	0.93	0.070	*

* = significant difference

ns = non-significant difference

TABLE 20: Regression parameters for the least squares regressions of weight on length (logarithmic scales) for smelt from the river Cree on a seasonal basis and for each age of fish.

smelt of an equivalent age.

The least squares regression parameters for the logarithmic relationship between weight and length are shown in Table 19 for the river Thames and Table 20 for the river Cree. Although the G.M. functional regression (Ricker, 1975) was not used, Nash (1982) showed that where weight and length were highly correlated ($r > 0.93$) the predictive and G.M. functional regressions were very similar.

It can be seen that in general the exponent 'b' was significantly different from 3 indicating allometric growth. The exceptionally high value for 'b' of 5.604 for Cree females in winter is presumably attributable to the increased weight for length resulting from maximal gonad development.

4:3:7 Condition

The variation in the mean condition factor is shown on a monthly basis in Figure 24 for smelt from the river Thames, and on a seasonal basis in Figure 25 for Cree smelt. In the case of the river Thames the data has been plotted for adults and juveniles, here defined as 0-group fish whose gonads show no clear evidence of development towards maturity, separately.

In the river Thames, the mean condition factor of all age groups of fish was higher in any given month in 1982 than was the case in 1981.

The somatic condition of adult female smelt from the Thames was relatively constant throughout the summer and winter months but declined sharply after the March 1982 sampling date. Gonad development was most rapid between December - March and resulted in

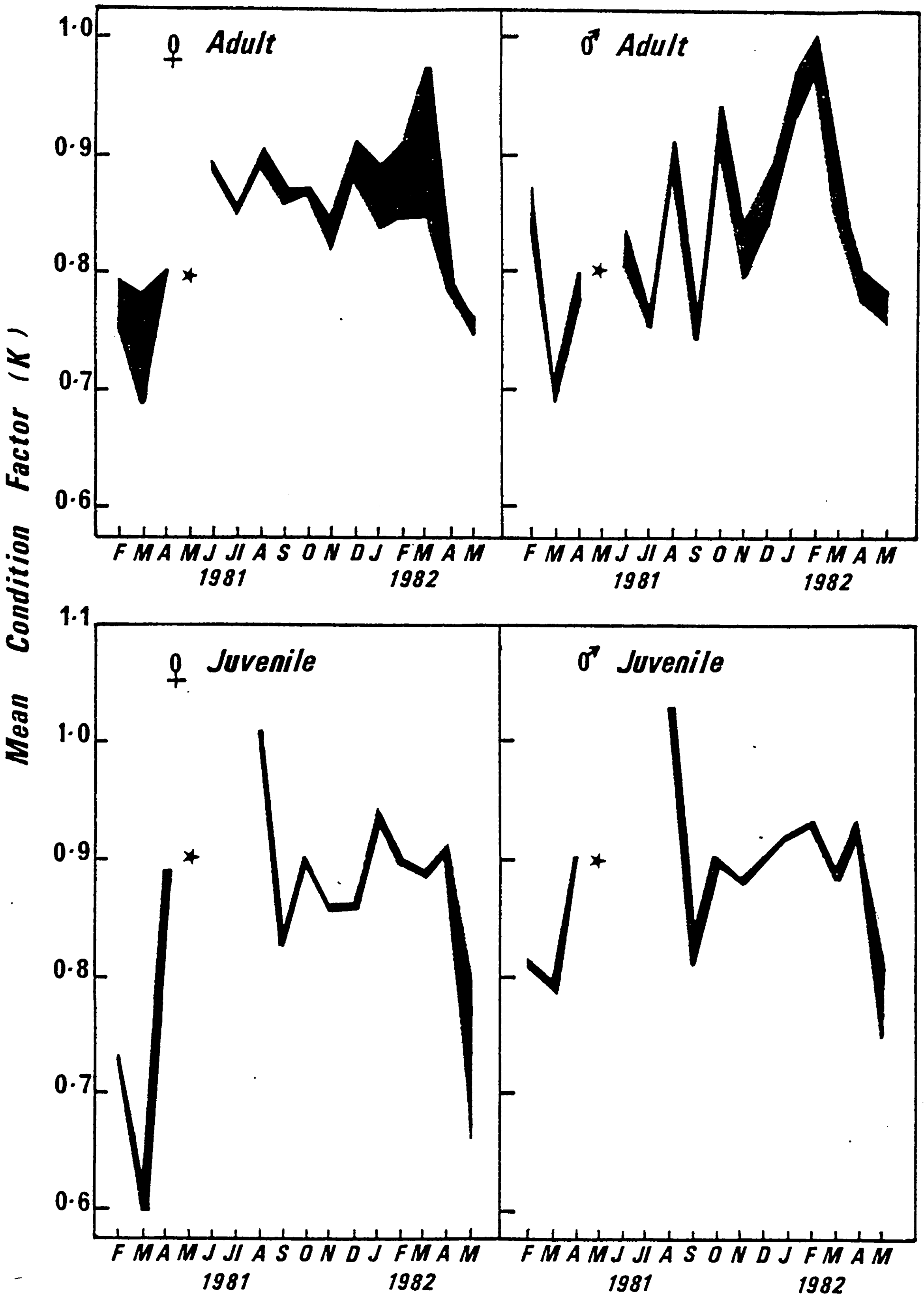


FIGURE 24: The seasonal pattern of condition in smelt from the river Thames. The top line represents total condition and the bottom line somatic condition. The distance between the two lines represents condition attributable to the gonads.

★ no samples.

	AGE (YEARS) 0+	1+	2+	3+
FEMALES	0.911 ± 0.029 (0.51 - 1.36)	0.849 ± 0.027 (0.47 - 1.32)	0.853 ± 0.028 (0.56 - 1.06)	0.861 (0.70 - 1.01)
MALES	0.901 ± 0.016 (0.64 - 1.34)	0.830 ± 0.021 (0.48 - 1.21)	0.859 ± 0.032 (0.53 - 1.20)	0.773 (0.74 - 0.81)
HERMAPHRODITES	0.975 (0.90 - 1.05)	0.830 ± 0.098 (0.54 - 1.19)	0.816 ± 0.109 (0.62 - 0.97)	-
SEXES COMBINED	0.905 ± 0.014 (0.51 - 1.36)	0.838 ± 0.018 (0.47 - 1.32)	0.854 ± 0.020 (0.53 - 1.20)	0.837 (0.70 - 1.01)

TABLE 21: The mean condition factor of smelt of different ages from the river Thames (± 95% confidence limits (if n ≥ 5) with range of values in parentheses).

	AGE (YEARS) 0+	1+	2+	3+
FEMALES	0.847 (0.81 - 0.88)	0.907 ± 0.020 (0.68 - 1.24)	0.876 ± 0.025 (0.60 - 1.35)	0.915 ± 0.125 (0.74 - 1.36)
MALES	0.79 -	0.885 ± 0.012 (0.65 - 1.15)	0.898 ± 0.016 (0.73 - 1.19)	0.924 ± 0.046 (0.78 - 1.09)
SEXES COMBINED	0.830 (0.79 - 0.88)	0.894 ± 0.010 (0.65 - 1.24)	0.888 ± 0.014 (0.60 - 1.35)	0.920 ± 0.055 (0.74 - 1.36)

TABLE 22: The mean condition factor of smelt of different ages from the river Cree (± 95% confidence limits (if n ≥ 5) with range of values in parentheses).

a peak in total condition in March. The decline in condition in April and May was presumably as a result of spawning. Adult male Thames smelt exhibited much wider fluctuations in condition than the females, and the influence of gonad development on total condition was less marked. Adult male smelt reached a peak of total condition one month earlier than the females (February 1982) and exhibited a marked decline in both somatic and total condition after this date. In both adult male and female Thames smelt there was no evidence that the development of gonads was at the expense of somatic condition.

Juvenile male and female Thames smelt exhibited similar patterns of condition which were free from the large fluctuations which characterised the cycle of condition in adult males. Juvenile smelt of both sexes reached a peak of condition in August 1981 and in the subsequent months the condition stabilised around 0.90. In both sexes there was a marked decline of both total and somatic condition from March - May 1982.

Table 21 shows the mean condition factor for each sex in the different age groups. There were insignificant differences between the mean condition of male and female Thames smelt in each age group. Furthermore the mean condition of hermaphrodites was not significantly different from that of either males or females in any age group. It can be seen that the mean condition of 0-group fish was higher than that for the other age groups.

Adult Cree smelt reached a peak of condition in the winter samples (February 1982) and as was the case in the Thames there was a marked reduction in both total and somatic condition after spawning. By the time the summer samples were collected condition had again started to increase. The influence of gonad development

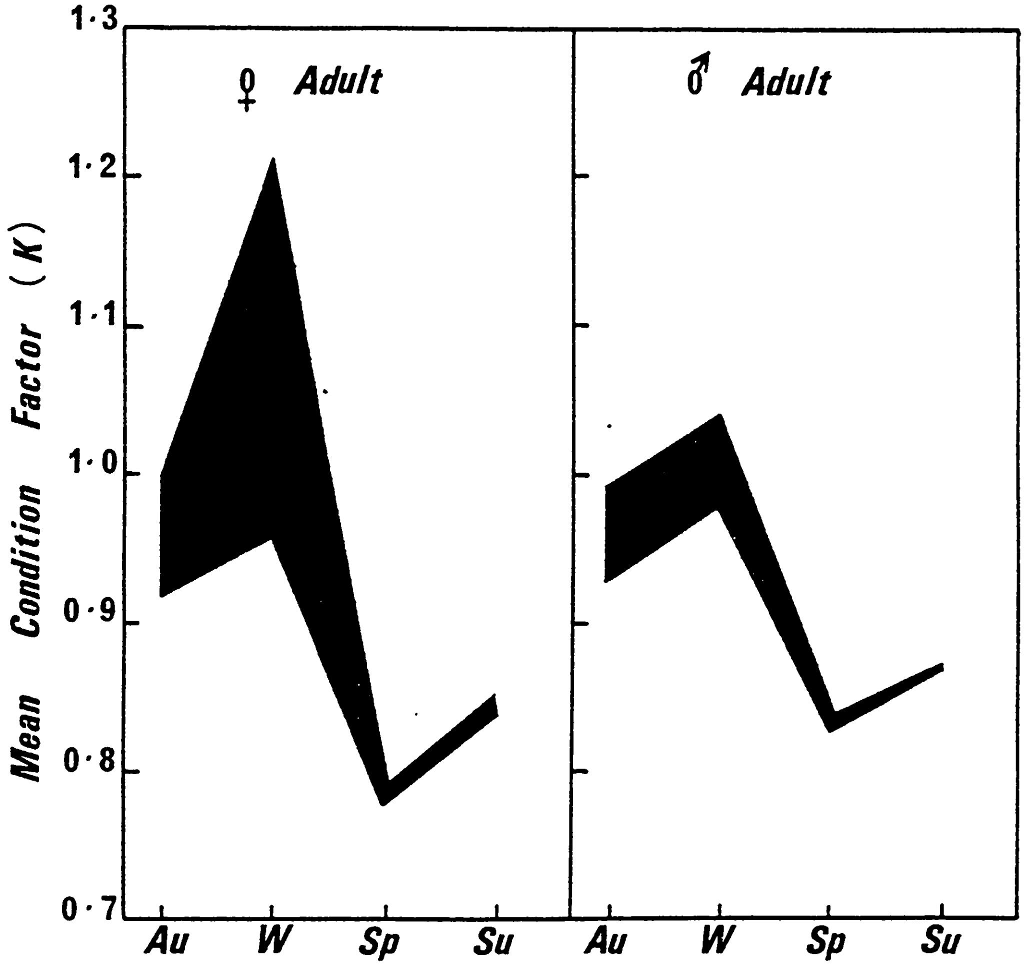


FIGURE 25: The seasonal pattern of condition in smelt from the river Cree.

on total condition was again very evident but as in the Thames, gonad development did not appear to be at the expense of somatic condition.

The mean condition of the different sexes of Cree smelt in each age group is shown in Table 22. The differences in mean condition between males and females were insignificant in all age groups. Mean condition was highest in 3+ year old Cree smelt.

Comparison of the mean condition of Thames and Cree smelt revealed insignificant differences in 0+ and 3+ year old fish. However, the mean condition of 1+ ($t = 6.21$, $p < 0.001$) and 2+ ($t = 4.68$, $p < 0.001$) year old Cree smelt was significantly higher than that for Thames smelt of the same age.

4:4 DISCUSSION

The longevity of smelt populations varies considerably between different localities (Belyanina, 1969). In general, small freshwater smelt do not survive for more than three years (Jensen, 1949; Belyanina, 1969) while individuals of twelve and even fifteen years of age have been found in the estuaries of the Yenisey, Lena, Anadyr and Khatanga rivers (Agapov, 1941)(in Belyanina, 1969).

The results from this study have shown that at both study sites the smelt exhibited a short-cycle life history, with only a small proportion of fish surviving into their fourth year of life. This is in close agreement with the findings of Masterman (1913), who found that less than 2% of the populations of smelt in the rivers Ouse and Nene survived into their fourth year. Furthermore, smelt in the Dee also appear to exhibit a similar life-span since only fish of 0+ - 3+ years old have been identified (Pearce, personal communication). Similar results were also presented by Rembiszewski (1970) who showed that in Poland the life-span of the majority of smelt, Osmerus eperlanus, did not exceed two or three years, although individuals of up to seven years of age were present at one study site (Miedwie Lake).

Warfel, Frost and Jones (1943) and McKenzie (1958) showed that estuarine smelt, Osmerus mordax, in north-eastern North America also exhibited a short-cycle life history with the populations comprising three prominent age groups, but with small numbers of individuals of four, five and six years of age being encountered.

Nikolsky (1963) considered that variations in life-span reflect the specific conditions of the environment for each stock. In Britain, conditions appear to favour a short-cycle life history.

Belyanina (1969) found that the maximal age of male smelt was two years less than that of females. No such trend was evident in the data from this study although there was a marked increase in the proportion of females in the older age groups. Similar shifts in sex ratio with age have been reported by many workers (Masterman, 1913; Schneberger, 1936; Beckman, 1942; Tremblay, 1946; Bailey, 1964; Belyanina, 1969; Burbidge, 1969; Saunders and Power, 1970a; Scott and Crossman, 1973).

Tremblay (1946) suggested that a higher post-spawning mortality rate in male smelt was responsible for the predominance of females in the older age groups and McKenzie (1964) showed that those smelt that died during spawning were predominantly males. A possible mechanism for this mortality was identified by Belyanina and Makarova (1965) who found that male smelt used up larger quantities of their pre-spawning, non-gonadal fat reserves in spawning activity. Burbidge (1969) believed that this decline in condition would render male smelt more susceptible to disease, parasites, predation, starvation and extreme weather conditions.

Bailey (1964) showed that in addition to a higher natural spawning mortality, male smelt were more prone to fishing mortality, both commercial and recreational, since a large proportion of the annual catch was taken during the periods when males dominated the spawning run. During the latter part of the run when females became more plentiful, the markets were glutted and the fishing effort was reduced (Bailey, 1964). A similar mechanism may also be operative in the river Cree since male smelt have been shown to remain on the spawning grounds longer than females (see Chapter 5) and are thus exposed to extended periods of exploitation.

Many studies of smelt, Osmerus spp., in both the estuarine and freshwater habitats, have shown that female smelt are larger than male smelt in any given age class (Masterman, 1913; Beckman, 1942; Warfel et al, 1943; Van Oosten, 1940; Baldwin, 1950; McKenzie, 1958; Hale, 1960; Lillelund, 1961; Bailey, 1964; McKenzie, 1964; Burbidge, 1969; Altukhov and Yerastova, 1974). Furthermore, many of the above named studies also showed that the length differences between the sexes became more marked with increasing age. Similar trends were evident from both study sites investigated in the course of this work. If the sex selective mortality referred to above was size selective for the larger male smelt then a mechanism for the increasing difference in length and weight between the sexes with increasing age would have been found.

Beckman (1942) showed that the differences between the lengths of the different sexes were very small and Burbidge (1969) found that although females exceeded the lengths of males in all age groups the difference was only significant in one age group. Similarly, Zilliox and Youngs (1958) found the difference between the sexes to be significant for 3+ and 5+ year old individuals and Altukhov and Yerastova (1974) concluded that in most cases the differences in length between the sexes were so small that the data could be pooled.

In contrast to the studies quoted above, Saunders and Power (1970a) and Jilek, Cassell, Peace, Garza, Riley and Siewart (1979) found that male smelt were larger than female smelt in the younger age groups but that this situation was reversed in the older fish.

Belyanina (1969) considered that all smelt populations could be divided into two groups depending on their pattern of growth through ontogeny. The first group consists of individuals whose growth is most intensive during the first year of life, followed by a comparatively sharp decrease in growth rate in later years. This group of smelt inhabits the temperate zone where a growing season of 6-7 months and an abundant supply of zooplankton enables rapid growth of the fry and young stages (Belyanina, 1969). The second group consists of individuals whose growth is comparatively slow in the first year of life but it increases in the second year and then decreases gradually. This group consists of smelt populations living under sub-arctic conditions where the later spawning period (May - July), lower temperatures and poorer food resources all affect the growth of 0-group fish. Changes of feeding habits in the second year of life result in improved growth (Belyanina, 1969).

Table 23 presents data on the instantaneous growth in length

LOCALITY	AGE (YEARS) 0	1	2	3	4	5	6	7	8	9	10
(a) FRESHWATER											
PSKOV-LAKE	4.28	3.37	3.47								
ILMEN LAKE	3.95	3.40	3.22								
VALDAY LAKE	3.97	3.83	2.56								
WHITE LAKE	4.09	3.22	3.22								
RYBINSK RESERVOIR	4.08	3.33	1.95								
KURISHES HAFF	4.14	3.74									
DADEY LAKE	4.26	3.58	2.71	2.71							
LAZMIADEN LAKE	4.41	2.40	3.22	2.40	3.37						
LADOGA LAKE	4.38	2.71	2.48	3.37	3.09	3.22					
ONEGA LAKE	4.14	3.22	1.79	2.48	1.39	1.10	1.61	1.61			
LAKE MICHIGAN	4.52	4.17	2.64								
CRYSTAL LAKE	4.68	4.13	2.93	2.53							
LAKE SUPERIOR	4.09	4.44	3.59	3.06	2.86	2.99					
(b) SEA-MIGRANT											
ELBE RIVER	4.26	4.14	3.66	3.66	3.26						
FINNISH GULF	4.36	3.50	3.22	3.18	2.77						
WHITE SEA: ONEGA BAY	3.85	3.99	3.78	3.85	3.69	3.74					
DVINA BAY	3.71	3.95	3.66	3.61	3.09	3.18	3.43	3.33	1.95		
KANDALAKSHA BAY	3.85	4.41	4.08	3.64	3.18	3.00					
CHESHA BAY	3.56	3.83	3.78	3.30	3.22	3.33	2.83				
YENISEY RIVER	3.81	3.97	3.76	3.56	3.30	3.00	2.77	1.61	2.40		
AMUR RIVER	4.01	4.09	3.56								
GREAT BAY, NEW HAMPSHIRE	4.39	4.08	3.26	3.89							
NORFOLK RIVERS	4.69	4.09	2.89	3.50							

TABLE 23: The instantaneous growth in length of selected populations of smelt (calculated from Belyanina, 1969).

for various populations of smelt, Osmerus spp.. In general, the results confirm the findings of Belyanina (1969) discussed above. Both populations investigated in this study show the pattern of growth typical of temperate smelt populations. However, several authors have reported that populations of smelt, Osmerus mordax, from temperate waters in North America exhibited the pattern of growth characteristic of more northerly populations (McKenzie, 1958; Bailey, 1964; Burbidge, 1969). These anomalies may be related to the time of spawning in these populations since in the Miramichi river smelt spawn from late April to early June (McKenzie, 1958) and in Lake Superior from mid-April to early May (Bailey, 1964). It seems possible that the lateness of the spawning season is at least partly responsible for the reduced growth in the first year. Support for this argument comes from the work of McKenzie (1958) who found that late hatching 0-group smelt bore scales with little or no sculpturing indicative of very poor growth in the first growing season.

Tables 24 and 25 present data for the growth in length of various populations of smelt from the estuarine and freshwater environment respectively. Limited conclusions can be drawn, and comparisons made, since in many cases details of the length measurement employed and of whether or not the data refer to length at age or mean length of age groups are not presented. Wherever possible, however, details of the methods employed have been included in the tables in order to assist comparison. The lack of comparability of the data is highlighted by the results from Matamek Lake which were based on a study between July - August. The low value of 16 mm quoted for one year old fish refers to fish which were 2-3 months old

STUDY SITES	AGE (YEARS) 1	2	3	4	5	6	7	8	COMMENTS
PSKOVSKO-CHUDSKOYE	72	97	129						*
ILMEN LAKE	47	82	107						*
WHITE LAKE	60	85	110						*
RYBINSK WATERBODY	59	87	94						*
DADEY LAKE	71	107	122						*
LAZMIADEN LAKE	82	93	118	127	156				*
KURISHES HAFF	63	105							*
ONEGA LAKE	63	88	94	106	110	113	118	133	*
LADOGA LAKE	80	95	107	136	158	183			*
PYAOZERA (KARELIA	-	-	106	113	122	129	136	144	*
GULL LAKE, MICHIGAN	60	150	163	180	198	187			**
LAKE CHAMPLAIN (Large Race)	165	209	248	169	183				**
CRYSTAL LAKE, MICHIGAN	113	175	194	206					***
CRYSTAL LAKE	92	157	171						***
MATAMEK LAKE	16	74	114	191	218	243	257	270	**
LAKE SUPERIOR	65	148	190	217	235	253	305		***
GREEN BAY, L. MICHIGAN	-	175	250	300	350				**
SOUTH BAY, L. HURON	-	141	160	185					**

* Not specified whether measurements refer to mean length of age groups or length at annulus formation
** Mean length of age groups
*** Length at annulus formation

TABLE 24: The growth in length (mm) of selected landlocked populations of smelt (modified from Belyanina, 1969).

STUDY SITES	1	2	3	4	5	AGE (YEARS) 6	7	8	9	10	11	12	COMMENTS
KURISHES HAFF	65	133	161	204									*
ELBE RIVER	71	134	173	212	238								*
NEVA RIVER	78	111	136	160	176								*
MIRAMICHI RIVER		145	165	187	206								**
YENISEY RIVER	46	98	141	176	203	223	239	244	255				*
LENA RIVER							196	234	263	276	288	301	*
CHESHA BAY	35	81	125	152	177	205	222						*
GULF OF OB				183	193	202	209	222					*
ONEGA BAY	47	101	145	192	232	274							*
DVINA BAY	41	93	132	169	191	215	246	274	281				*
KANDALAKSHA BAY	47	129	188	226	250	270							*
GREAT BAY, NEW HAMPSHIRE	86	145	171	220									**
ZATOKA POMORSKA		79	97										**
ZALEW WISLANY			157	175									**
OUSE & NENE, NORFOLK	114	174	192	225									**
RIVER THAMES	91	135	168	196									***
	112	140	162	178									***
	89	132	154										***
RIVER CREE	130	196	230	249									***
	117	192	221										***

* Not specified whether measurements refer to mean length of age groups or length at annulus formation
** Mean length of age groups
*** Length at annulus formation

TABLE 25: The growth in length (mm) of selected estuarine populations of smelt (modified from Belyanina, 1969).

Table 24 presents growth in length data for several lacustrine smelt populations, and it can be seen that the Russian landlocked populations are characterised by short-cycle life histories and small maximal lengths (< 150 mm). In contrast, the populations from North American lakes, particularly the Great Lakes, exhibit growth rates in close accordance with those exhibited by estuarine populations. Table 25 shows that in general estuarine smelt populations do not exceed 300 mm in length. Growth rates in the temperate populations are much more rapid than in the arctic populations which are characterised by increased longevity but reduced growth rate. Maximal lengths however appear much less variable than in the landlocked populations.

Cree smelt had a higher growth rate than any of the other populations shown in Table 25, reaching 249 mm in length after only three years growth. In contrast, Thames smelt together with the populations from the Neva river, Zatoka Pomorska, Zalew Wislany and the Miramichi river showed below average growth. Stunted growth ie. the exhibition of an individual growth rate well below the potential for the species, is a well known feature of certain fish (Burrough and Kennedy, 1979). Carlander (1966) considered that population density, in relation to the carrying capacity of the habitat, was the major environmental factor controlling the growth of individual fish and intra-specific competition has frequently been considered to be a major factor affecting the growth rate of smelt. Abrosov and Agapov (1957) believed that declining growth rates of smelt were a result of increasing population density and Lillelund (1961) and Belyanina (1969) considered that, in general, strong year classes grew more slowly than weak ones. However, McKenzie (1958) compared the annual larval production from the Miramichi system with the average length of the same fish when they entered the fishery and found that there was no relationship between growth rate and year class abundance. The results from the river Thames support this finding since fish of the 1981 year class exhibited significantly higher growth rates than the 1980 year class despite the apparent strength of the 1981 year class.

Rupp and Redmond (1966) showed that the abundance of the plankton fauna had a pronounced effect on the growth rate of smelt, Osmerus mordax. In view of the ichthyofaunal diversity and abundance in the Thames (see Chapter 2) it is tempting to speculate that competition may be the cause of the reduced growth rate of smelt in the Thames. Sedgwick (1979) considered that competition for food was unlikely to occur amongst any of the feeding groups of fish which he identified in the Thames estuary (see Chapter 6). However, it is possible that the feeding relationships in the Thames have become aggravated by the increase in diversity and abundance of fish species in the estuary since Sedgwick's (1979) study, the field work for which was carried out during the early stages of recolonisation of the tideway (1973/74). Unfortunately, no further studies of the feeding relationships in the Thames estuary have been carried out. The improved growth rate of the abundant 1981 year class would suggest that mechanisms other than competition for food are responsible for the stunted nature of Thames smelt.

Rembiszewski (1970) while acknowledging the importance of feeding conditions concluded that differences in growth rate in the same lake in different years were mainly attributable to delayed spawning as a result of the prevailing meteorological variables.

Temperature has been identified as a major determinant of smelt growth rate by Kirpichnikov (1935) and Belyanina (1969). McKenzie (1958) showed that the year class with the largest fish at two years of age was hatched earliest following an early spawning run, while the year class with the shortest fish was hatched latest. The less variable nature of growth in the river Cree may reflect the constancy of the timing of spawning (spawning started on 10.03.80; 10.03.81; 11.03.82 and 10.03.83). However, in view of the temperature regime in the river Thames (see Chapter 2) it seems unlikely that this accounts for the difference in growth between the two study sites.

Rupp and Redmond (1966) considered that one of the most striking features of smelt, *Osmerus mordax*, in the inland waters of Maine was the variability in the life history which it exhibits in allopatric populations. Rupp (1959) concluded that these differences might be the result of differing genetic constitutions ie. allopatric speciation which had proceeded far enough to form distinct racial groups with characteristic habitat tolerances, growth rates, maximum lengths and spawning behaviour. Such a mechanism may also be used to account for the large difference in growth rates between the Thames and Cree populations. However, controlled experimental introductions from six established populations into eight new environments by Rupp and Redmond (1966) resulted in these authors concluding that the growth and abundance of smelt in a given environment depends more on environmental factors than on any supposed genotypic differences among stocks. Transfer studies were not possible during the course of this study but in view of the results of Rupp and Redmond's (1966) transfers it would appear that environmental factors present in the Thames result in reduced growth rates. Sedgwick (1979) considered that in a complex environment such as a polluted estuary, stress factors may result in the death of an organism or be more subtle and cause a reduction in growth.

Kendall (1927) believed that the lakes of New England, including Lake Champlain, contained two distinct sizes of smelt designated "large" and "small" in the literature. In Sebago Lake for example, the "large" smelt may reach lengths of 250 - 375 mm while the "small" smelt seldom exceed 150 mm. Furthermore, the two forms spawn at different times, up to one month apart. While no anatomical basis has been found on which to separate the races, their growth patterns are characteristically distinct. Greene (1930) found that the "small" race matured after two winters while only one in three of the "large" race matured at this age. Zilliox and Youngs (1958) found that the "large" race had a longevity of six years while the "small" race had a normal life-span of only four winters.

The "small" smelt - "large" smelt theory had been a laymans tradition in New England since the mid-nineteenth century (Rupp and Redmond, 1966) but Kendall's (1927) report was the first in the scientific literature. Despite the circumstantial nature of Kendall's (1927) evidence the theory was widely accepted and added to in further studies. Kendall (1927) concluded that transfer studies should be carried out to determine the relationship of the two forms.

The transfer studies of Rupp and Redmond (1966) described on the preceding page showed that environment and not genotype exerted the most influence on growth. However, one transfer provided an "unexpected" result in that a number of smelt with growth rates much higher than in any previous collection or in the parent lake were identified. The only characteristic of transferred smelt that provided evidence of genotypic control was the time of spawning with all transferred populations maintaining the spawning time of their parent populations (Rupp and Redmond, 1966). These authors considered that if early spawning fish maintained their racial integrity through the reproductive isolation afforded by retention of the early spawning habit when introduced to a lake containing late spawners, then a mechanism for allowing the continued existence of the two stocks of smelt in the same lake would have been determined.

Kendall (1927) provided evidence of separate spawning periods and Cheney (1876) reported that large scale introductions and transfers of smelt from water to water were common in Maine as early as 1870. These introductions, both authorised and unauthorised, were still occurring as recently as 1966 (Rupp and Redmond, 1966).

CHAPTER 5: REPRODUCTIVE BIOLOGY

5:1 INTRODUCTION

The scant attention that has been paid to smelt in the British scientific literature is highlighted by the almost total lack of data regarding their reproductive biology. Most of the information that does exist is concerned with the period and site of spawning (eg. Parnell, 1838; Day, 1884; Buckland, 1891; Regan, 1911; Wheeler, 1979) and the appearance of the spawn in the rivers (eg. Parnell, 1938). The only quantitative data regarding reproductive biology is that provided by Masterman (1913) who listed the percentage weight of the ovaries or testes to that of body weight for the months December - April.

The objectives of this chapter are threefold:

i) To investigate the course of gonad development throughout the annual cycle in order to quantify the reproductive investment, and to determine the fecundity of smelt. Increased attention is being given to the number of eggs developing in mature fish (Bagenal and Braum, 1978) since fecundity is one of the most important aspects of the life history of a species (Alvarez-Lajonchere, 1982). A knowledge of fecundity is desirable in both fish culture and fisheries management (Lagler, 1956) and in studies of fish mortality, racial characterisation, population estimates, population dynamics and productivity studies (Bagenal and Braum, 1978). The age and size at first maturity were also investigated.

ii) To investigate the population dynamics of spawning run smelt with regard to size and age structure, and sex ratios. The duration of the run and possible factors involved in initiating the run were also investigated. Observations of the spawning run, while lacking quantitative support, were also made.

iii) It was intended to investigate aspects of spawning site selection and egg deposition densities during the 1982 spawning run using burlap covered enamel tiles as described by Rothschild (1961). Unfortunately, the fragmentary nature of the run in that year prevented such a study. However, the duration of the incubation period of smelt eggs was investigated at various temperatures in the laboratory and used to supplement observations on the first appearance of prolarvae in the estuary.

5:2 METHODOLOGY

The course of development of the gonads of smelt was traced by using the gonad and somatic weights, obtained as described in Chapter 2, to calculate the gonadosomatic ratio (GSR = gonad weight/ body weight excluding gonads) (Gibson and Ezzi, 1978).

In contrast to the findings of McKenzie (1958), Bailey (1964), Burbidge (1969) and Saunders and Power (1970a, 1970b) the sex of even the smallest 0-group smelt could be determined, in most cases by viewing through a binocular microscope (X8), but in the largest individuals (> 90 mm) by gross examination. This enabled the size at which smelt first attain sexual maturity to be determined.

The ovaries of mature females, which had been preserved in Simpson's (1951) modification of Gilson's fluid, were shaken periodically to aid separation of the ova from any ovarian tissue present in the samples. Bagenal and Braum (1978) recommended this preservative since it breaks down ovarian tissue and assists liberation of the eggs which become hardened by the solution and are therefore easier to count. Bailey (1964) preserved the ovaries of smelt, *Osmerus mordax*, in alcohol but experienced considerable difficulties in counting the eggs because of "their small size and tendency to stick together". Gilson's fluid effectively resolved the latter of these problems. Furthermore, ova preserved in this way can be stored for several months without disadvantage.

Prior to enumeration, the Gilson's fluid was decanted from the ova and replaced by successive changes of water. This process removed small fragments of ovarian tissue and any minute recruitment stock oocytes which would have matured in subsequent years (Bagenal, 1969). Large sections of ovarian tissue were removed manually with forceps, after having first liberated any ova contained therein. When thoroughly washed, the eggs were filtered under pressure using a Buchner flask and funnel and spread out on filter paper to dry. Aggregations of eggs were prevented from forming by moving the ova about manually and when thoroughly dry the eggs were stored in open petri dishes which allowed their moisture content to equilibrate with the air. Total counting of the ova was not possible so fecundity estimates were derived by Simpson's (1951) dry weight sub-sampling technique. Three random sub-samples of 200 eggs were counted under a binocular microscope and the weights of the sub-samples, and of all the ova, were determined (± 0.1 mg). In general, the variability in weight of the sub-samples was <5%. However, occasionally one sub-sample was markedly heavier or lighter than the other two, in which case the sub-sample was retaken. Absolute fecundity (F) was then calculated using the expression:

$$F = \frac{W \times 200}{\bar{w}}$$

W = dry weight of all the ova
$\bar{w}$ = mean dry weight of the sub-samples

Relative fecundity, defined as the number of eggs per gram total weight of fish (Mann and Mills, 1979), was also calculated.

Oocyte diameters (10 from each fish) were measured by viewing on a Mikrops microprojector (see Chapter 4) at a magnification of X55, as described by Bailey (1964). The maximum diameter of the egg was measured since they were rarely of regular shape. Although the water hardened diameter of fertilised ova, as used by Pope, Mills and Shearer (1961), is the most appropriate measure of the space and reserves available for the developing embryo (Mills, personal communication), the preserved diameter can be used to gain an insight into variations in egg size between different size groups or populations of fish (eg. Gibson and Ezzi, 1978, 1979, 1980, 1981; Treasurer, 1981; Turnpenny, Bamber and Henderson, 1981; Nash, 1982).

The ovotestes from hermaphroditic smelt were prepared for histological examination using the following procedure. The tissue was dehydrated in a graded alcohol series (70% - absolute) and transferred to terpineol which is miscible with paraffin wax. After soaking in paraffin wax for four hours the ovotestes were blocked in paramat pastillated wax (melting point = 56-57° C) and sectioned (10 μm) using a Cambridge Shandon rotary microtome. The resultant tissue ribbons were stained using haematoxylin and eosin in the following series: xylene (15 mins.); absolute, 95% and 70% ethanol (5 mins. each); 50% ethanol and distilled water (2 mins. each); haematoxylin (3 mins.); running water (15 mins.); eosin (2 mins.); 70% and 95% ethanol (1 min. each); absolute ethanol and 1:1 xylene:absolute ethanol (3 mins. each); xylene (15 mins.).

The stained sections were then mounted in DPX mountant (BDH Microscopical Reagents) on glycerine-albumen coated slides and examined microscopically.

The duration of the period of incubation of smelt eggs was determined experimentally in the laboratory. Fertilised ova were obtained by stripping three female and four male smelt obtained from the river Cree on 15.03.82 and held in the Department's hatchery until 19.03.82. The 'dry' method of fertilisation was employed and the fertilised ova were stirred with a feather for 10 minutes prior to thorough washing. 0.5 ml of fertilised ova were then introduced to one litre incubation jars (bottom surface area = 66.5 cm^2) which contained 0.75 l of deionised water. In practice, considerable difficulty was experienced in handling and decanting the ova and considerable variation in deposition densities resulted (see Table 26). This was in contrast to a similar experiment conducted by Hulbert (1974) who obtained remarkably consistent densities using the same procedure.

Each incubation jar was then fitted with a screw-top lid which had previously been drilled to permit the entry of an air-line and the removal of prolarvae. Three incubation temperatures were investigated, the details of which together with the number of replicate jars, ranges of egg densities and hatching success are shown in Table 26.

The two lowest temperatures were maintained by placing the incubation jars in heated water baths located in a thermostatically controlled cold room (5 ± 1° C). The highest temperature regime was maintained in the laboratory by balancing the antagonistic effect of a heated water bath fitted with a cooling coil.

Throughout the incubation period, the eggs were observed three times daily and any prolarvae which had hatched were removed to an aquarium using a teat pipette.

Fungal infection of the eggs was first noticed five days post-fertilisation in the 15° C temperature regime. All replicates at all temperatures were therefore immediately treated with a 2ppm bath of zinc-free malachite green for one hour (Roberts and Shepherd, 1974). This treatment proved successful at the two lowest temperatures, but despite re-application failed to control the fungus at 15°C. This uncontrolled fungus appeared to be the cause of the low percentage hatch at this temperature. Richardson and Belknap (1934) also found it difficult to check fungal growth using salt and Scott's mercurochrome and they concluded that planting of smelt, *Osmerus mordax*, by incubating eggs in a hatchery required "complicated techniques" if fungus was to be avoided. Belyanina (1969) believed that one of the major natural causes of egg mortality was *Saprolegnia spp*.

Mean Temperature (°C)	6.0	10.1	15.1
Temperature Range	4.5 - 7.0	7.5 - 12.0	14.5 - 16.0
No. of Replicates	6	6	4
Mean Egg Density (cm^{-2})	6.7	10.1	18.1
Range of Egg Densities	2.8 - 11.4	5.2 - 16.2	10.6 - 24.9
Mean % Hatch	26.6	20.6	10.0
Range of % Hatch	12.0 - 44.3	0.9 - 52.6	8.0 - 12.0

TABLE 26: Details of the temperature regimes, number of replicates, egg densities and percentage hatch from the egg incubation experiment.

5:3 RESULTS

5:3:1 The Seasonal Pattern Of Gonad Development

The pattern of gonad development, as indicated by the mean gonadosomatic ratio, is shown on a monthly basis in Figure 26 for the river Thames, and on a seasonal basis in Figure 27 for the river Cree.

In the river Thames, the mean gonadosomatic ratio of adult female smelt peaked in March in both 1981 and 1982 and then fell

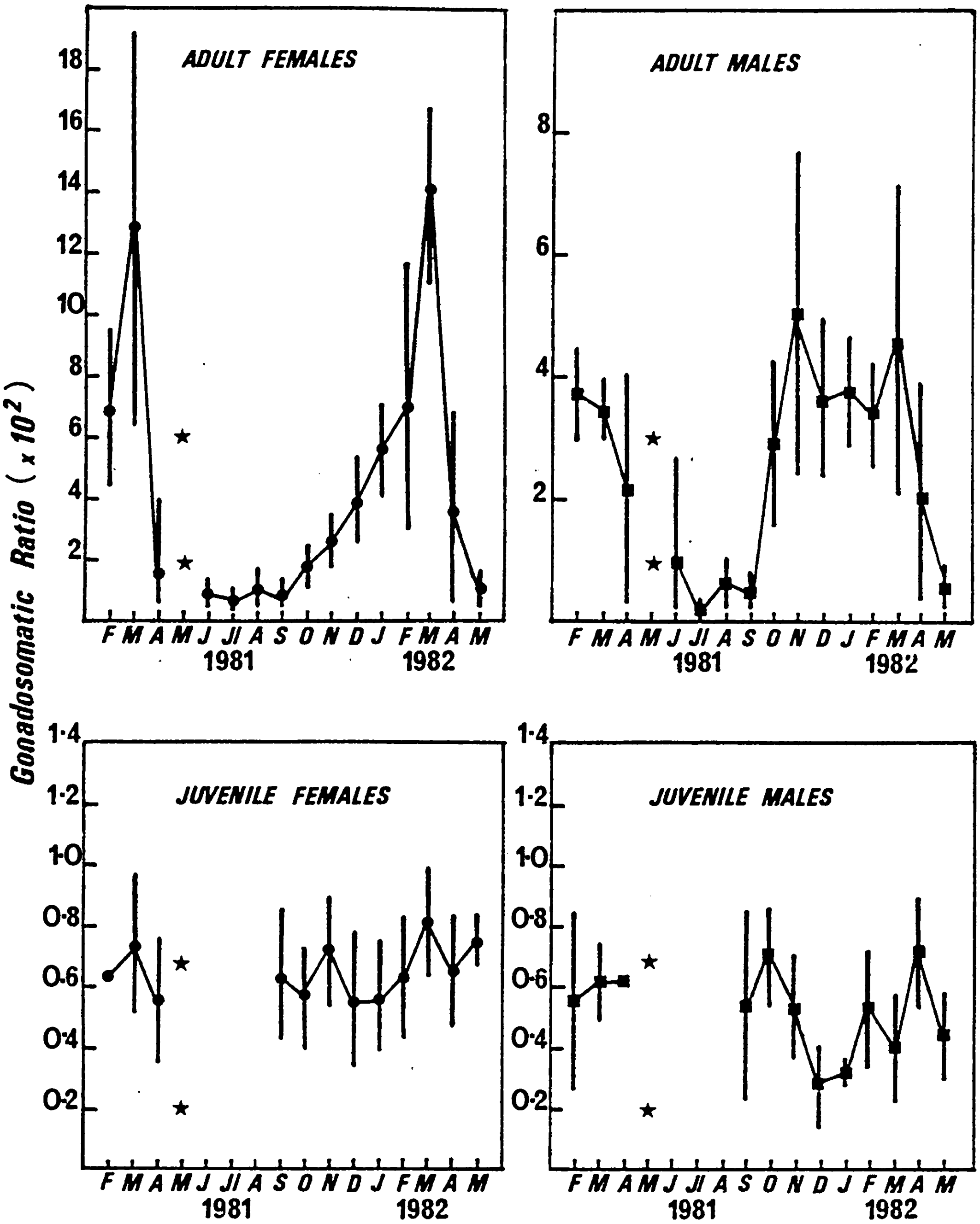


FIGURE 26: The seasonal variation in mean gonadosomatic ratio for Thames smelt. Vertical bar represents ± 1 S.D.

★ no samples.

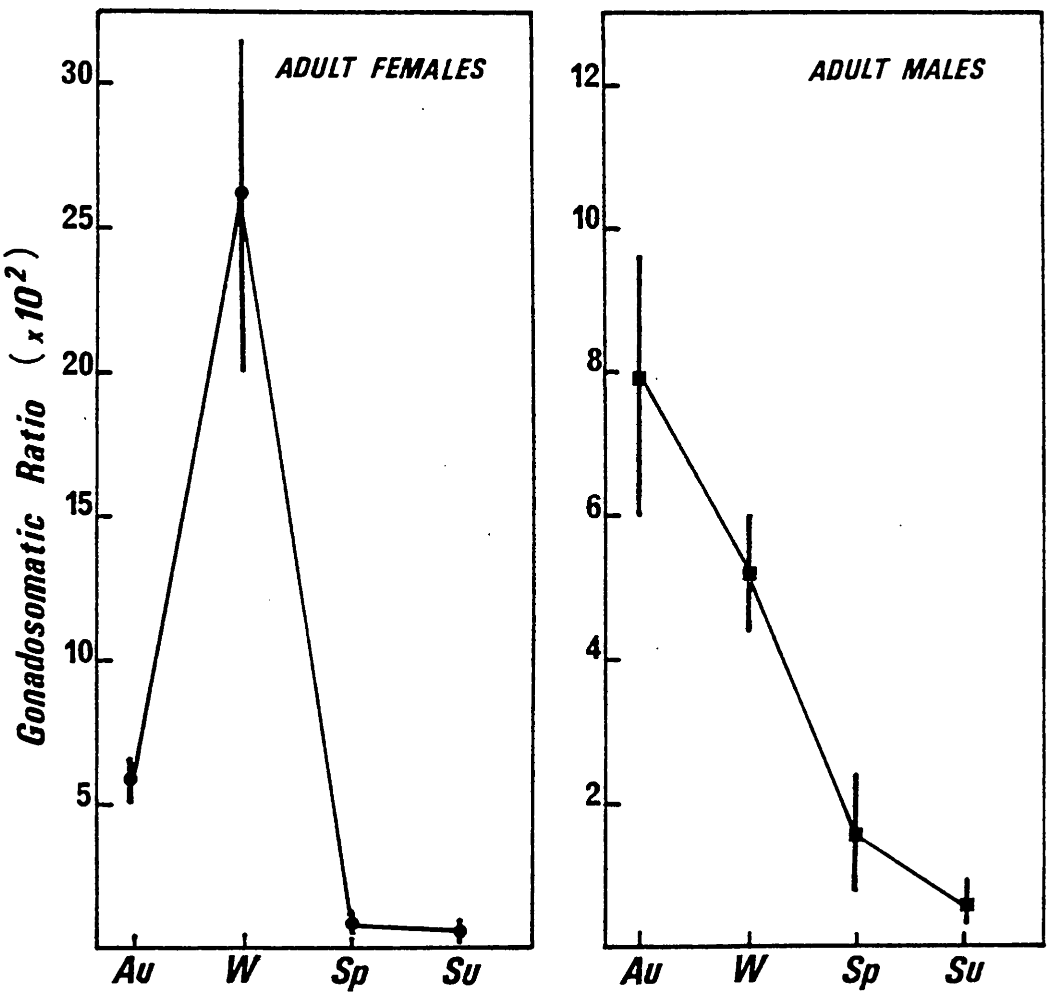


FIGURE 27: The seasonal variation in mean gonadosomatic ratio for Cree smelt. Vertical bars represent ± 1 S.D.

sharply in April. Throughout the summer and early autumn there was little development of the ovaries but gonad development increased markedly between September - February and extremely sharply between February - March. The variation around the mean gonadosomatic ratio increased in the months February - April, presumably as a result of differing degrees of reproductive investment in the pre-spawning period, and the degree of spawning success and efficiency of resorption of unshed gametes in the post-spawning period.

The development of the testes of adult male Thames smelt increased rapidly between September - November 1981, with testicular development peaking in November 1981. A high level of testicular development was maintained from November 1981 - March 1982 (in contrast to the sharp peak that occurred in adult females) and there was a marked reduction in April and May 1982. The peak value of the mean gonadosomatic ratio for adult males was approximately one third that for adult females.

Juvenile Thames smelt exhibited a seasonal pattern of gonad development free from the wide fluctuations characteristic of the adult population. However, there were fluctuations in the mean gonadosomatic ratio, particularly among juvenile males. Thus, mean gonadosomatic ratio values ranged from 0.56 - 0.81 for juvenile females and 0.29 - 0.71 for juvenile males.

In the river Cree, the mean gonadosomatic ratio of adult females reached a peak at the time the winter samples were taken and declined sharply in spring. As was the case in the Thames, adult male smelt from the Cree reached a peak of gonad development prior to the females and there was a decline in mean gonadosomatic ratio prior to spawning.

The mean reproductive investment in adult Cree females was

	AGE (YEARS)						
	0+		1+		2+		3+
FEMALE	2.88 ± 4.40 (0.45 - 22.88)		12.63 ± 2.92 (1.96 - 40.40)		7.67 ± 2.93 (1.91 - 45.38)		5.49 (3.22 - 7.77)
		t = 3.51 **		t = 2.41 *		t = 0.33 ns	
MALE	1.33 ± 0.64 (0.18 - 8.11)		4.58 ± 0.65 (0.37 - 8.59)		6.98 ± 1.13 (3.20 - 10.47)		5.23 (2.70 - 7.76)
		t = 7.18 ***		t = 3.97 ***		t = 0.15 ns	

TABLE 27: The mean gonadosomatic ratio for smelt of all ages from the river Thames in March ($\pm$ 95% confidence limits (if $n \geq 5$)). Details of hermaphroditic individuals are given in Table 43.

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns = non-significant.

	AGE (YEARS)						
	0+		1+		2+		3+
FEMALE	-		23.57 ± 4.64 (12.11 - 31.50)		29.59 ± 4.69 (24.79 - 34.13)		35.03 (34.42 - 35.65)
				t = 1.49 ns		t = 1.77 ns	
MALE	-		5.22 ± 0.32 (3.56 - 6.87)		5.35 ±0.58 (3.95 - 6.69)		4.99 (4.36 - 5.74)
				t = 0.45 ns		t = 0.80 ns	

TABLE 28: The mean gonadosomatic ratio of smelt of all ages from the river Cree in winter (February 1982). ($\pm$ 95% confidence limits (if $n \geq 5$).

approximately double that of adult female Thames smelt. Masterman (1913) found that the mean condition of gonad development (equivalent to the gonadosomatic ratio) could reach the high value of 23.2%, presumably for females. Lillelund (1961) found that the relative weight of ripe ovaries (to body weight) varied from 18 - 22%. These values are in close agreement with those from the Cree. The peak value of gonadosomatic ratio for adult Cree males was approximately 50% greater than the corresponding figure for Thames smelt. However, at the time of spawning males from both environments had closely similar mean gonadosomatic ratios which were in close agreement with the values obtained by Masterman (1913) and Lillelund (1961).

The mean gonadosomatic ratio of each age group of smelt prior to spawning is shown in Table 27 for the river Thames and Table 28 for the river Cree. Cree females had significantly ($p < 0.001$) higher mean gonadosomatic ratios than Thames females in all age groups. The differences between Thames and Cree male smelt were generally insignificant although 2+ year old Thames smelt had significantly higher mean gonadosomatic ratios than Cree smelt of the same age ($t = 2.82$, $p < 0.01$).

5:3:2 Length And Age At First Maturity

Smelt from the river Cree were never found to reach sexual maturity in their first year of life although very limited numbers of 0-group fish were examined. However, 0-group specimens were never observed in the spawning migrations and the youngest fish present on the spawning grounds had spent two winters in the estuary (see Section 5:3:5).

In contrast, mature 0-group specimens were identified from the river Thames, particularly amongst fish of the 1981 year class.

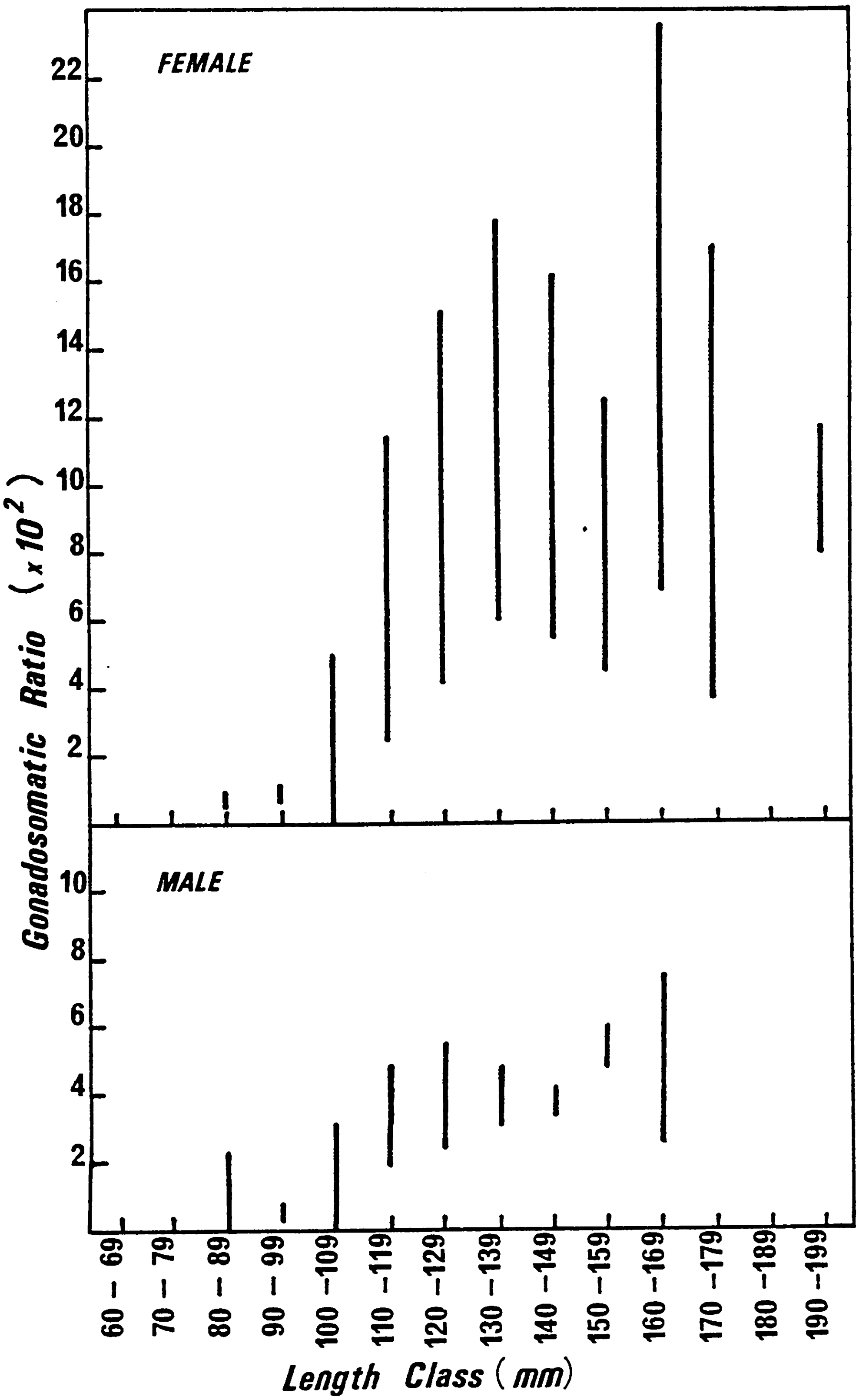


FIGURE 28: The range of gonadosomatic ratios for each 10 mm length group of Thames smelt, expressed as ± 1 standard deviation from the mean. The data were derived from samples taken in February and March, 1981 and 1982.

PLATE 8: Mature 0-group female and male (bottom) smelt from the 1981 year class from the river Thames.

The samples from February and March 1981 and 1982 were used to determine the length of Thames smelt at first maturity by plotting the mean gonadosomatic ratio for 10 mm size groups, the results of which are presented in Figure 28.

In female Thames smelt there appeared to be a distinct mature group consisting of individuals belonging to the 110 - 119 mm size group and above, and an immature group consisting of all fish belonging to size groups below the 100 - 109 mm size group. The 100 - 109 mm size group appeared to be somewhat intermediate and contained both mature and immature specimens. The mean gonadosomatic ratio increased sharply between the 100 - 109 and 120 - 129 mm size groups and then appeared to level off.

The situation was less well defined in male Thames smelt although similarities were evident. Again, the 100 - 109 mm size group contained both immature and mature specimens, but in addition one mature male smelt was identified from the 80 - 89 mm size group.

Table 29 presents data showing the proportion of mature fish in each size category for 1981 and 1982. It can be seen that, with the exception of the one mature specimen in the 80 - 89 mm size group, fish first reached sexual maturity in the 100 - 109 mm size group and that all fish in the 120 - 129 mm size group were mature. In 1981, only one mature 0-group smelt was identified, a mature male in the 80 - 89 mm size class. In 1981 however, the improved growth rate of 0-group smelt resulted in a higher occurrence of precociously mature individuals. Sexual maturity in 0-group fish appears to be dependent on the fish achieving lengths of greater than 100 mm in their first year of life. However, in 1981 50% of 1+ year old females reached maturity in the 100 - 109 mm size group while no 0+ year old females of the 1981 year class were mature in the same size class. Similarly, 100% of 1+ year old females reached maturity in the 110 - 119 mm size group but only 33% of 0+ year old females reached maturity in the same size class. Thus achievement of maturity in the smaller size groups is not only dependent on length but is age dependent as well.

	PROPORTION OF SEXUALLY MATURE FISH (%)			
SIZE CLASS	MALE 1981	FEMALE 1981	MALE 1982	FEMALE 1982
60 - 69	0	-	-	-
70 - 79	0	-	0	-
80 - 89	20	-	0	0
90 - 99	0	0	0	0
100 - 109	64#	50#	50	0
110 - 119	89#	100#	100*	33
120 - 129	100#	100#	100*	100*

0+ year old unless stated
* includes both 0+ and 1+ year old fish
\# 1+ year old fish only

TABLE 29: The proportion of sexually mature fish of both sexes in the smaller size classes of Thames smelt in February and March 1981 and 1982.

5:3:3 Fecundity

The logarithmic relationships between fecundity and several independent variables are shown in Table 30 for the river Thames and Table 31 for the river Cree. In addition, the logarithmic relationship between fecundity and fork length is shown graphically in Figure 29 for both the Thames and Cree data. Logarithmic plots have the advantage of stabilising the variance with regard to fish size (Pope _et al_, 1961) and the linear relationship allows standard statistical techniques to be used (Bagenal and Braum, 1978).

	a	b ± 95% CL's	r	n
FORK LENGTH	-2.0165	2.8816 ± 0.2150	0.8777	45
SOMATIC WEIGHT	2.9690	0.9008 ± 0.2083	0.8856	45
GONAD WEIGHT	3.9617	0.5680 ± 0.2848	0.7727	45
AGE	3.9035	0.8981 ± 0.4177	0.3650	45

TABLE 30: Least squares regression parameters for the logarithmic relationships between fecundity and several independent variables for smelt from the river Thames.

	a	b ± 95% CL's	r	n
FORK LENGTH	-5.1866	4.2261 ± 0.1221	0.9528	16
SOMATIC WEIGHT	1.9596	1.3743 ± 0.1240	0.9512	16
GONAD WEIGHT	3.5228	0.8306 ± 0.0996	0.9687	16
AGE	4.1769	1.3700 ± 0.2039	0.8616	16

TABLE 31: Least squares regression parameters for the logarithmic relationships between fecundity and several independent variables for smelt from the river Cree.

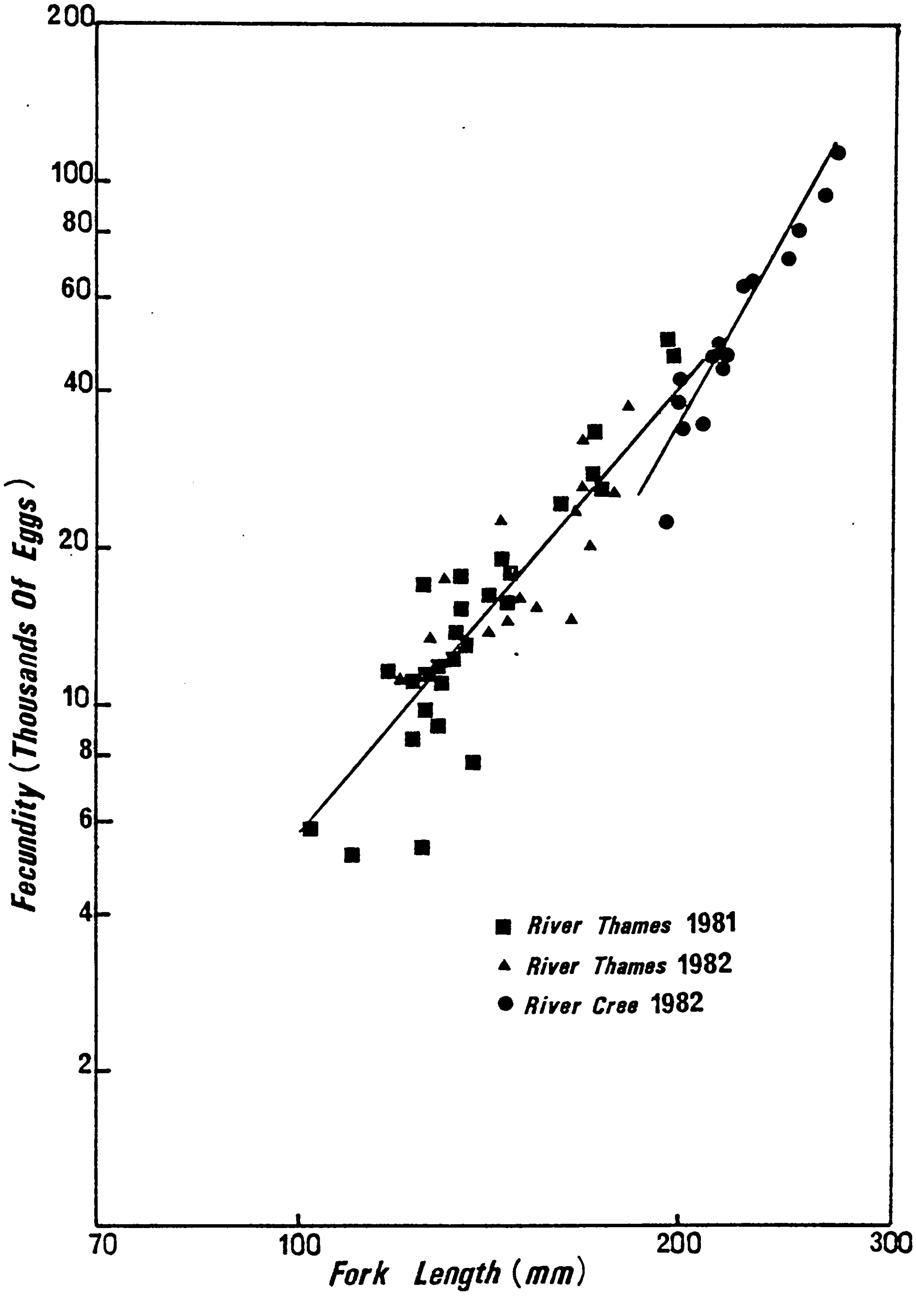


FIGURE 29: The relationship between fecundity and fork length for smelt from both the river Thames and river Cree [logarithmic co-ordinates]. (See text for details of regression parameters).

	AGE (YEARS)			
	0+	1+	2+	3+
(a) RIVER THAMES:				
MEAN FECUNDITY	8719	16115	26003	24254
STANDARD ERROR	1299.59	1089.84	3231.43	-
COEFFICIENT OF VARIATION(%)	33.3	43.3	46.5	-
n	5	41	14	1
(b) RIVER CREE:				
MEAN FECUNDITY	-	40131	66512	105956
STANDARD ERROR	-	2887.6	5691.9	10813.5
COEFFICIENT OF VARIATION(%)	-	21.6	19.1	14.4
n	-	9	5	2

TABLE 32: The mean fecundity for smelt of various ages from both the river Thames and the river Cree.

Bagenal and Braum (1978) indicated that b usually has a value of 3 when fecundity is related to length and may be about 1 when related to weight or age.

In the river Thames, the logarithmic relationship of fecundity on length gave a regression coefficient b of 2.8816 with upper and lower 95% confidence limits of 3.097 and 2.6666 respectively. The relationships between fecundity and somatic weight and age were linear with regression coefficients of 0.9008 (0.6925 - 1.1091) and 0.8981 (0.4804 - 1.3158) respectively. In contrast, the relationship between fecundity and gonad weight was not linear in Thames smelt and the regression coefficient had a value of 0.5680 which was significantly different from 1. Bagenal (1967) explained the lack of proportionality between fecundity and gonad weight by considering that either heavy ovaries produced larger and therefore fewer eggs, or the ovarian connective tissue increased disproportionately in larger ovaries.

In the river Cree, the regression coefficient for the logarithmic relationship between fecundity and fork length was significantly different from 3. Furthermore, the regression coefficients for the logarithmic relationships between fecundity and somatic weight, gonad weight and age were all significantly different from 1.

There was considerable variation in the fecundity of smelt within each age group at both study sites and Wilkinson and Jones (1977) showed that the median fecundity of each age group of dace, Leuciscus leuciscus, was described by a second degree polnomial. The mean fecundity of each age group of smelt from both the Thames and Cree is shown in Table 32.

In the river Thames, all independent variables were significantly correlated with the dependent variable fecundity.

	FECUNDITY	FORK LENGTH	SOMATIC WEIGHT	GONAD WEIGHT	AGE
FORK LENGTH	0.8777	-	-	-	-
SOMATIC WEIGHT	0.8856	0.9509	-	-	-
GONAD WEIGHT	0.7727	0.7754	0.8203	-	-
AGE	0.3650	0.5009	0.5294	0.2585	-

Tabulated r for n = 45, p = 0.05 r = 0.2888; p = 0.001 r = 0.465

TABLE 33: Correlation coefficients for the relationships between fecundity and various independent variables, and between the variables themselves for smelt from the river Thames.

	FECUNDITY	FORK LENGTH	SOMATIC WEIGHT	GONAD WEIGHT	AGE
FORK LENGTH	0.9528	-	-	-	-
SOMATIC WEIGHT	0.9512	0.9730	-	-	-
GONAD WEIGHT	0.9687	0.9374	0.9176	-	-
AGE	0.8616	0.8878	0.9272	0.8257	-

Tabulated r for n = 16, p = 0.05 r = 0.468; p = 0.001 r = 0.708.

TABLE 34: Correlation coefficients for the relationships between fecundity and various independent variables, and between the variables themselves for smelt from the river Cree.

However as Table 33 shows, all independent variables, with the exception of age and gonad weight, were highly significantly correlated ($p < 0.001$) with each other. Similarly in the river Cree, all independent variables were highly significantly correlated ($p < 0.001$) both with fecundity and with each other. This correlation between independent variables means that an apparent relationship between fecundity and any of the independent variables may actually be the result of the correlation between two or more independent variables. Multiple regression was therefore used to control for this confounding effect (SPSS, 1975) thereby allowing evaluation of the contribution of specific variables.

The results of the multiple regression analysis on fecundity data for smelt from the river Thames are shown in Tables 35-39.

In the four factor analysis shown in Table 35 age, fork length and surprisingly gonad weight contributed insignificantly to the prediction of fecundity. Somatic weight was the only significant variable. The multiple regression equation based on these four variables accounted for 81.41% of the observed variation in fecundity. Gonad weight, which had the lowest variance ratio (F) was removed from the analysis resulting in the three factor analysis shown in Table 36 and which accounted for 81.22% of the observed variation in fecundity. Fork length again contributed insignificantly to the prediction equation and was omitted, resulting in the two factor analysis shown in Table 37. This equation accounted for 79.93% of the variation but age still failed to contribute significantly to the prediction equation. It would therefore appear that the most advantageous terms for the prediciton equation are derived from the logarithmic relationship between fecundity and somatic weight which accounts for

TABLE 35: Logarithmic Multiple Regression of Fecundity Against Somatic Weight, Age, Fork Length, Gonad Weight (River Thames)

VARIABLE		MULTIPLE R	MULTIPLE R^2	ΔR^2	B	F	P	BETA
SOMATIC WEIGHT	(X_1)	0.88561	0.78430	0.78430	0.5402	4.218	$p < 0.05$	0.5311
AGE	(X_2)	0.89403	0.79928	0.01498	-0.3034	2.045	ns	-0.1233
FORK LENGTH	(X_3)	0.90125	0.81225	0.01219	1.2219	2.853	ns	0.3722
GONAD WEIGHT	(X_4)	0.90227	0.81408	0.00183	0.0590	0.394	ns	0.0803

$$\text{Log } Y = 0.9022 + 0.5402 \log X_1 - 0.3034 \log X_2 + 1.2219 \log X_3 + 0.0590\ X_4; \quad R^2 = 81.41\%$$

TABLE 36: Logarithmic Multiple Regression of Fecundity Against Somatic Weight, Age, Fork Length (River Thames)

VARIABLE		MULTIPLE R	MULTIPLE R^2	ΔR^2	B	F	P	BETA
SOMATIC WEIGHT	(X_1)	0.88561	0.78430	0.78430	0.6220	7.518	$p < 0.01$	0.6115
AGE	(X_2)	0.89403	0.79928	0.01498	-0.3518	3.212	ns	-0.1430
FORK LENGTH	(X_3)	0.90125	0.81225	0.01297	1.2078	2.832	ns	0.3679

$$\text{Log } Y = 0.8622 + 0.6220 \log X_1 - 0.3518 \log X_2 + 1.2078 \log X_3; \quad R^2 = 81.22\%$$

TABLE 37: Logarithmic Multiple Regression of Fecundity Against Somatic Weight and Age (River Thames)

VARIABLE		MULTIPLE R	MULTIPLE R^2	ΔR^2	B	F	P	BETA
SOMATIC WEIGHT	(X_1)	0.88561	0.78430	0.78430	0.9785	139.369	$p < 0.01$	0.9619
AGE	(X_2)	0.89403	0.79928	0.01498	-0.3550	3.134	ns	-0.1443

$$\text{Log } Y = 2.9817 + 0.9785 \log X_1 - 0.3550 \log X_2; \quad R^2 = 79.93\%$$

TABLE 38: Logarithmic Multiple Regression of Fecundity Against Total Weight, Fork Length and Age (River Thames)

VARIABLE		MULTIPLE R	MULTIPLE R^2	ΔR^2	B	F	P	BETA
TOTAL WEIGHT	(X_1)	0.89133	0.79446	0.79446	0.6220	7.946	$p < 0.01$	0.6262
FORK LENGTH	(X_2)	0.89630	0.80336	0.00889	1.1191	2.353	ns	0.3409
AGE	(X_3)	0.90216	0.81390	0.01054	-0.2929	2.321	ns	-0.1191

$$\text{Log } Y = 1.004 + 0.6220 \log X_1 + 1.1191 \log X_2 - 0.2929 \log X_3; \quad R^2 = 81.39\%$$

TABLE 39: Logarithmic Multiple Regression of Fecundity on Total Weight and Fork Length (River Thames)

VARIABLE		MULTIPLE R	MULTIPLE R^2	ΔR^2	B	F	P	BETA
TOTAL WEIGHT	(X_1)	0.89133	0.79446	0.79446	0.5923	7.040	$p < 0.05$	0.5963
FORK LENGTH	(X_2)	0.89630	0.80336	0.00889	1.0169	1.900	ns	0.3097

$$\text{Log } Y = 1.1682 + 0.5923 \log X_1 + 1.0169 \log X_2; \quad R^2 = 80.34\%$$

78.43% of the observed variation in fecundity.

Unfortunately, somatic weight can only be determined by killing the fish and if the fish are to be returned to the water variables which can be measured without damage to the fish would be more useful in predictions. The multiple regressions were therefore repeated using total weight instead of somatic and gonad weights. The three factor analysis of fecundity against total weight, fork length and age is shown in Table 38. Fork length and age contributed insignificantly to this regression and age was subsequently omitted resulting in the two factor analysis shown in Table 39. Fork length was still insignificant and the most advantageous prediction equation for fecundity would therefore appear to be the logarithmic relationship between fecundity and total weight* which accounts for 79.45% of the observed variation in fecundity.

The results of the multiple regression analysis on the fecundity data from the river Cree are shown in Tables 40 - 42.

In the four factor analysis shown in Table 40 neither age nor somatic weight contributed significantly to the prediction of fecundity. Statistics were not calculated for the variable fork length because the F - level was insignificant. The derived prediction equation accounted for 96.32% of the variation in fecundity. Age was omitted from the analysis and the resulting two factor analysis is shown in Table 41. Both gonad weight and somatic weight contributed significantly to the prediction of fecundity and the multiple regression, which had been reduced to its most advantageous terms, accounted for 96.30% of the observed variation in fecundity.

As was the case in the Thames however, gonad weight cannot be measured unless the fish are killed and total weight was therefore

* Log Fecundity = 0.8854 log total weight + 2.9477

TABLE 40: Logarithmic Multiple Regression of Fecundity Against Gonad Weight, Somatic Weight, Age and Fork Length (River Cree)

VARIABLE		MULTIPLE R	MULTIPLE R^2	ΔR^2	B	F	P	BETA
GONAD WEIGHT	(X_1)	0.96874	0.93847	0.93847	0.51511	18.096	$p < 0.01$	0.6008
SOMATIC WEIGHT	(X_2)	0.98135	0.96305	0.02459	0.62865	4.184	ns	0.4351
AGE	(X_3)	0.98145	0.96325	0.00020	0.06030	0.064	ns	-0.0379
FORK LENGTH	(X_4)	F - Level insufficient for computation						

$$\text{Log } Y = 2.7388 + 0.5151 \log X_1 + 0.6286 \log X_2 + 0.0603 \log X_3; \quad R^2 = 96.32\%$$

TABLE 41: Logarithmic Multiple Regression of Fecundity Against Gonad Weight and Somatic Weight (River Cree)

VARIABLE		MULTIPLE R	MULTIPLE R^2	ΔR^2	B	F	P	BETA
GONAD WEIGHT	(X_1)	0.96874	0.93847	0.93847	0.52027	20.474	$p < 0.01$	0.6068
SOMATIC WEIGHT	(X_2)	0.98135	0.96305	0.02459	0.56990	8.652	$p < 0.05$	0.3944

$$\text{Log } Y = 2.8256 + 0.5203 \log X_1 + 0.5699 \log X_2; \quad R^2 = 96.30\%$$

TABLE 42: Logarithmic Multiple Regression of Fecundity Against Total Weight, Age and Fork Length (River Cree)

VARIABLE		MULTIPLE R	MULTIPLE R^2	ΔR^2	B	F	P	BETA
TOTAL WEIGHT	(X_1)	0.96937	0.93968	0.93968	1.46835	47.600	$p < 0.01$	1.1340
AGE	(X_2)	0.97198	0.94474	0.00506	-0.28521	1.191	ns	-0.1794
FORK LENGTH	(X_3)	F - Level insufficient for computation						

$$\text{Log } Y = 1.7277 + 1.4683 \log X_1 - 0.2852 \log X_2; \quad R^2 = 94.47\%$$

substituted for gonad and somatic weights. In the three factor analysis shown in Table 42 age and fork length contributed insignificantly to the prediction of fecundity. The logarithmic relationship between fecundity and total weight* accounted for 93.97% of the variation in observed fecundity and if the fish are to be returned alive to the water this equation provides the most advantageous method of prediction.

Data regarding the relative fecundity of smelt from the two study sites is presented in Figure 30. Within each study site there does not appear to be any clear relationship between relative fecundity and size although the relative fecundity of Cree smelt was markedly lower than in the Thames. Since relative fecundity is reciprocally related to egg size (Altukhov and Yerastova, 1974) it appears that egg size is not related to fish size within either study site, but that Cree smelt produce larger eggs than smelt from the Thames.

The data presented in Figure 31 shows that preserved egg diameters from Cree smelt had a mean diameter of 0.75 mm while the mean diameter of eggs from Thames smelt was 0.57 mm. Within either of the study sites however, there was no clear relationship between egg size and fish size although when the data were pooled from both sites egg size showed a tendency to increase sharply with size up to 200 mm and then level off.

5:3:4 Hermaphroditism

During the course of this study, a total of 21 hermaphroditic smelt were recorded from the river Thames. Details of these fish are

*Log Fecundity = 1.2551 log total weight + 2.0657

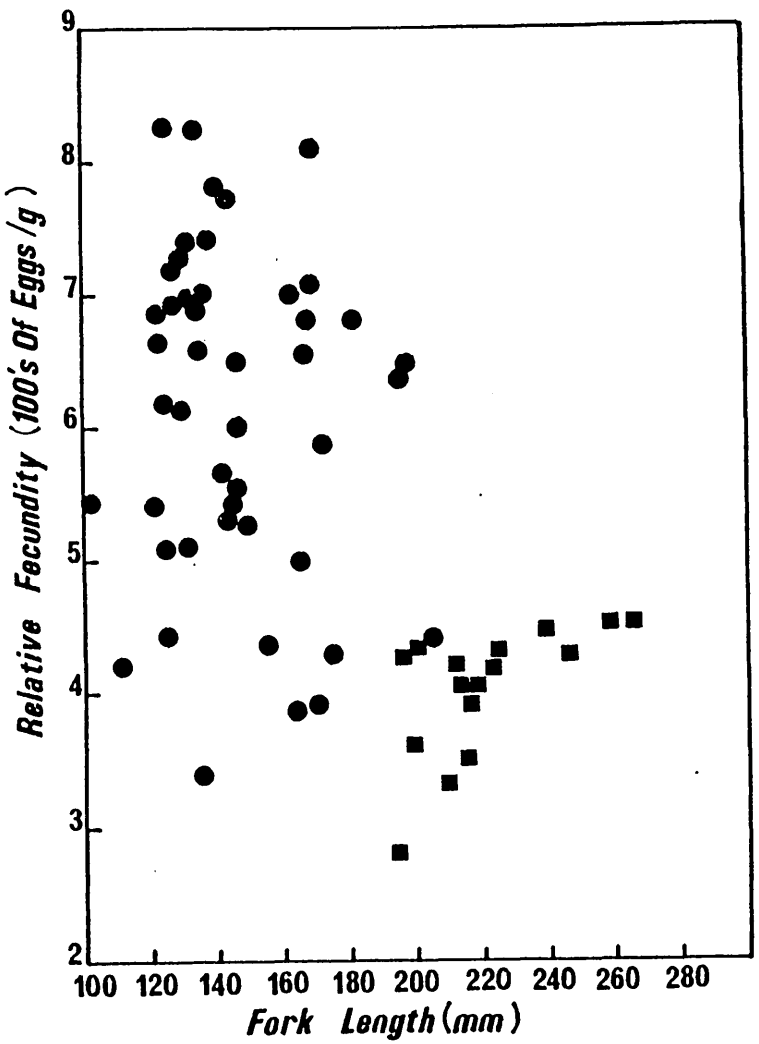


FIGURE 30: The relationship between relative fecundity and fork length for Thames (●) and Cree (■) smelt.

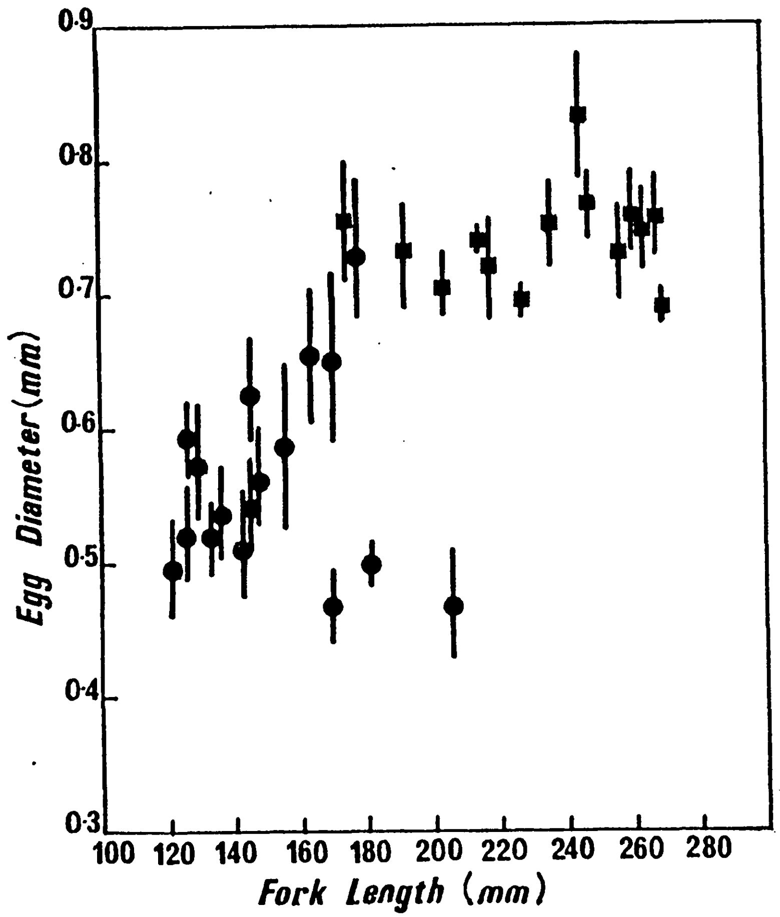
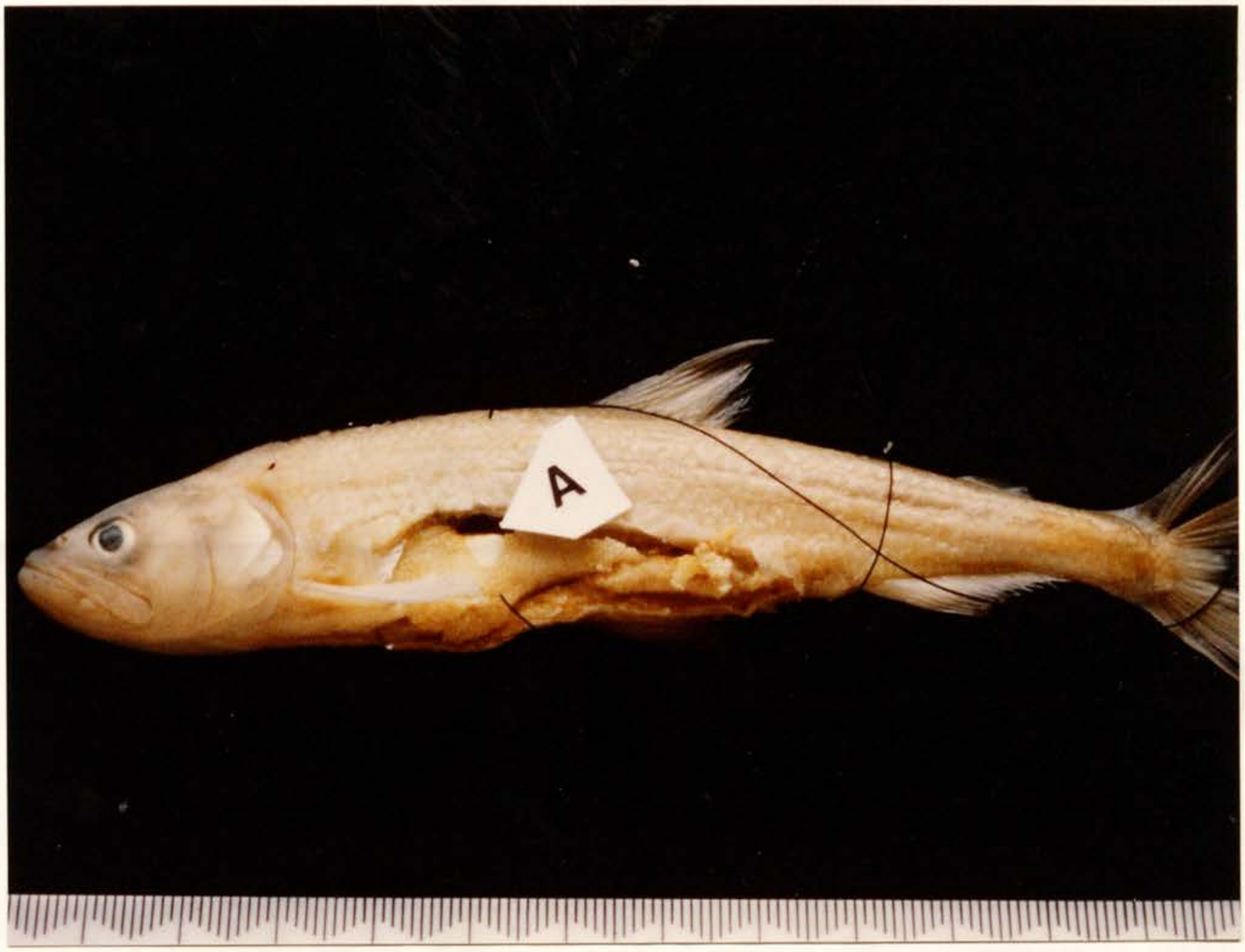


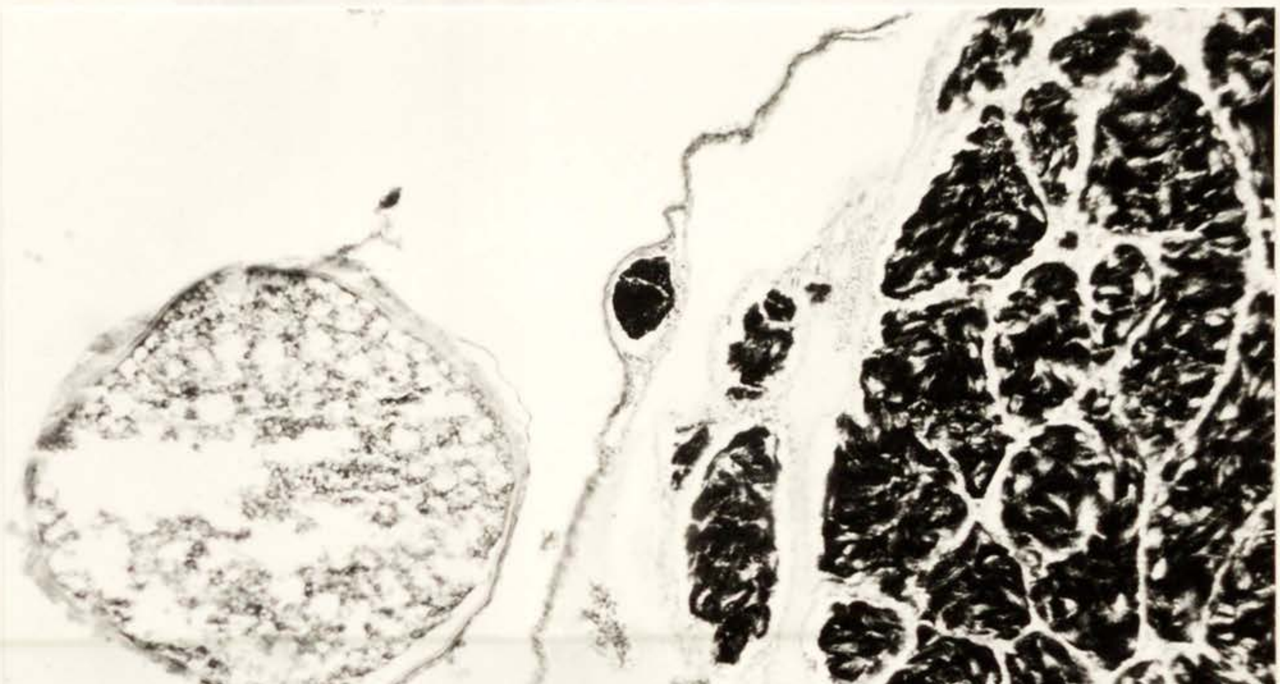
FIGURE 31: The relationship between egg diameter and fork length for Thames (●) and Cree (■) smelt. Vertical bars represent ± 1 S.D.

DATE OF CAPTURE	FORK LENGTH mm	TOTAL WEIGHT g	K	AGE	YEAR CLASS	GONADOSOMATIC RATIO OVARIAN	TESTICULAR	TOTAL	FECUNDITY	PREDICTED FECUNDITY*	DEVIATION FROM PREDICTED FECUNDITY	EXTERNAL APPEARANCE
090281	136	22.1	0.88	1+	1979	-	-	-	-	-	-	Female
090281	142	24.1	0.84	1+	1979	11.9	1.7	13.6	14760	14592	+168	Female
090281	130	21.0	0.96	1+	1979	6.1	2.6	8.7	8836	13410	-4574	Female
020381	123	16.4	0.88	1+	1979	19.3	1.5	20.8	8965	9761	-796	Female
020381	101	5.6	0.54	1+	1979	-	-	-	-	-	-	Female
070481	104	9.1	0.81	1+	1979	-	-	-	-	-	-	-
070481	119	11.8	0.70	1+	1979	3.6	0.7	4.3	-	-	-	-
070481	114	12.8	0.86	1+	1979	8.0	1.8	9.8	-	-	-	-
040681	142	20.8	0.73	2+	1979	-	-	-	-	-	-	-
020781	147	19.7	0.62	2+	1979	4.2	0.1	4.3	-	-	-	-
020781	152	29.9	0.85	2+	1979	0.6	0.4	1.0	-	-	-	-
020781	137	19.0	0.74	2+	1979	0.4	0.1	0.5	-	-	-	-
160981	152	31.8	0.91	2+	1979	2.8	0.2	3.0	-	-	-	-
021081	153	34.6	0.97	2+	1979	5.3	1.2	5.5	-	-	-	-
021181	123	13.6	0.73	1+	1980	-	-	-	-	-	-	-
151281	113	15.2	1.05	0+	1981	-	-	-	-	-	-	-
280182	113	13.0	0.90	0+	1981	3.8	0.5	4.3	8250	9036	-786	-
120382	168	42.0	0.89	2+	1979	-	-	-	-	-	-	Female
120382	121	21.1	1.19	1+	1980	7.5	0.8	8.3	9317	13512	-4195	Female
260482	151	27.0	0.78	1+	1980	3.0	3.2	6.3	-	-	-	-
260482	147	25.0	0.79	1+	1980	1.9	0.1	2.0	-	-	-	-

* Predicted from: Log Fecundity = 2.9690 + 0.9008 Log somatic weight.

TABLE 43: Fork length, total weight, condition factor, age, year class, gonadosomatic ratio and fecundity of the hermaphroditic smelt from the river Thames. Details of the date of capture, the external appearance and deviation from the predicted fecundity are also shown.





PLATES 9 & 10: Hermaphroditism from the river Thames.

Top: The gross morphological appearance of the ovotestis of an hermaphroditic Thames smelt. The testicular component is labelled (A).

Bottom: The histological appearance of a transverse section of ovotestis (x 120).

presented in Table 43.

Externally the fish all resembled mature females and lacked the nuptial tubercles which are a male secondary sexual character. Internal examination revealed that the ovotestes were predominantly ovarian in nature (see Plate 9), but in addition there were small areas of testicular tissue which in general were located in the anterior half of the ovotestis. In the majority of hermaphroditic specimens the ovarian component contributed between 60 - 97.7% of the weight of the ovotestes. However, in April 1982 an hermaphroditic individual in which the testicular component contributed 52% of the total weight of the ovotestis was identified. As with the other specimens this fish did not possess nuptial tubercles although it may have done at spawning time. The histological appearance of an ovotestis is shown in Plate 10.

Hermaphroditism was particularly prevalent amongst fish of the 1979 year class (15 individuals) but hermaphroditic specimens were also identified from the 1980 (4 individuals) and 1981 (2 individuals) year classes.

Comparison of the fecundity of hermaphroditic smelt with that of gonochoristic specimens was restricted by the small number of hermaphrodites taken immediately prior to spawning, and by the need to examine the ovotestes histologically. However, Table 43 shows that in most cases the hermaphroditic individuals had lower fecundities than the values predicted by the logarithmic relationship between fecundity and somatic weight.

5:3:5 Spawning Run Population Dynamics

The account below deals only with data derived from sampling

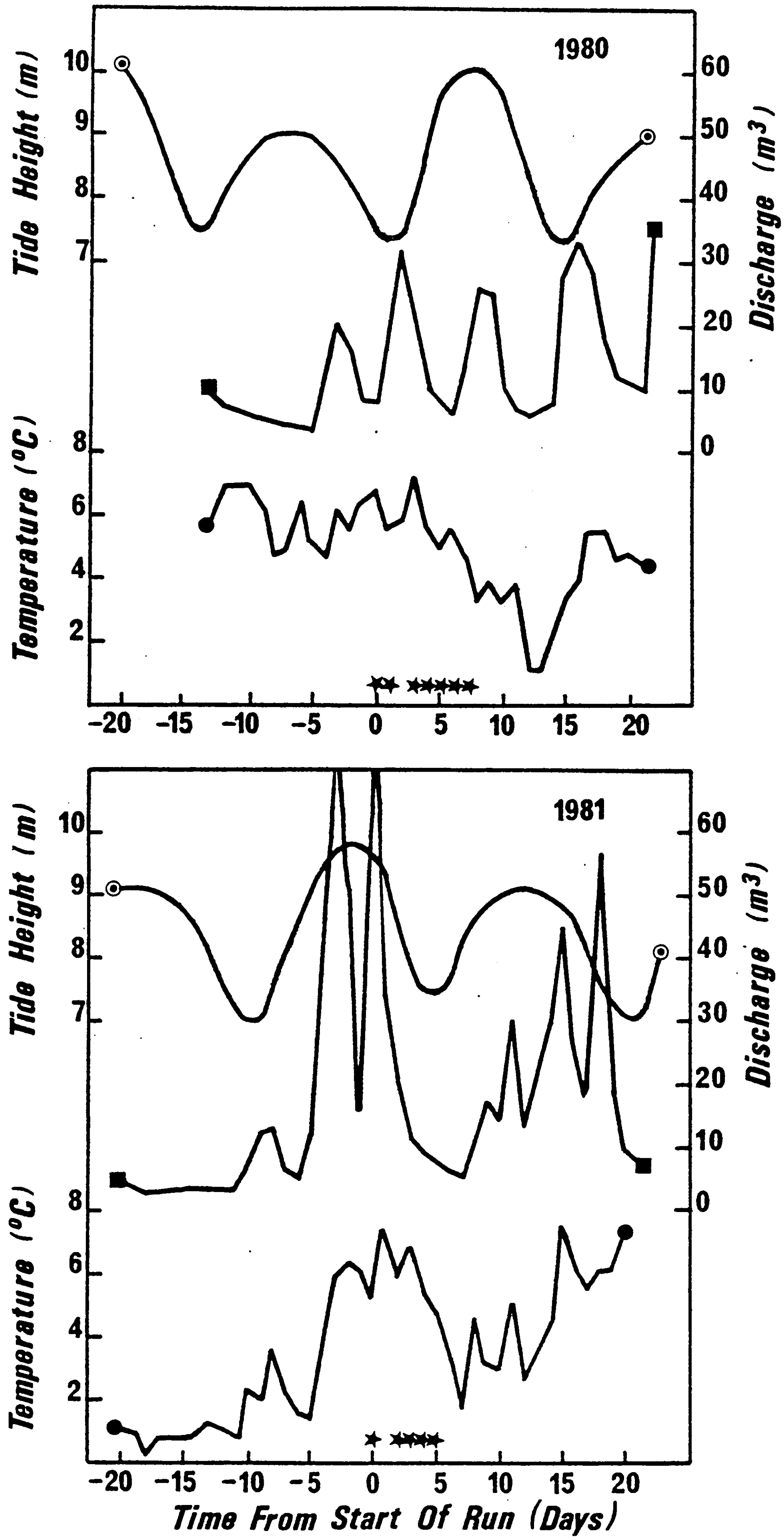


FIGURE 32: Mean daily tide height (⊙), mean daily discharge (■) and mid-afternoon (1500 hrs) water temperature (●) for the river Cree in the period leading up to and following entry of smelt into the river. (★ fish present in river).

the spawning runs into the river Cree.

Figure 32 presents data for water temperatures (taken at 1500 hours daily), mean daily discharge (m^3) and mean daily tide height (m) on a daily basis from mid-February to the end of March. The periods when fish were present in the river has also been indicated.

In 1980, smelt were first detected in the vicinity of the spawning grounds on 10.03.80 although it is possible that they entered after nightfall on 09.03.80. The fish left the river on 12.03.80 following a marked rise in water level but returned on 13.03.80 after the flood peak had fallen. Small numbers of fish were present until 16.03.80 when the last samples were obtained from the river.

In 1981, the fish were again first detected in the river on 10.03.81 but entry may also have occurred during the night. Very high flows were present from mid-morning on 10.03.81 and the fish left the river. They re-entered on 12.03.81 and were present in the river until 15.03.81 when very small numbers were observed some 0.75 km below the A75 roadbridge.

In both years, temperatures in the river were above 5°C at the time of entry but the mean daily tide height varied from 7.5 m (1980) to 9.5 m (1981). Many of the local fishermen expressed a belief that the fish ascended the river with the highest spring tides. Appendix 2 shows the date of the first appearance of smelt in the river Cree in the period 1926 - 1981 and it can be seen that fish entered the river on all phases of the tide.

The duration of the spawning run in the Cree was approximately one week. However, in both years the run was interrupted for approximately 24 hours by high flows and fish were only actually present in the river for 6 days in 1980 and 5 days in 1981. On the

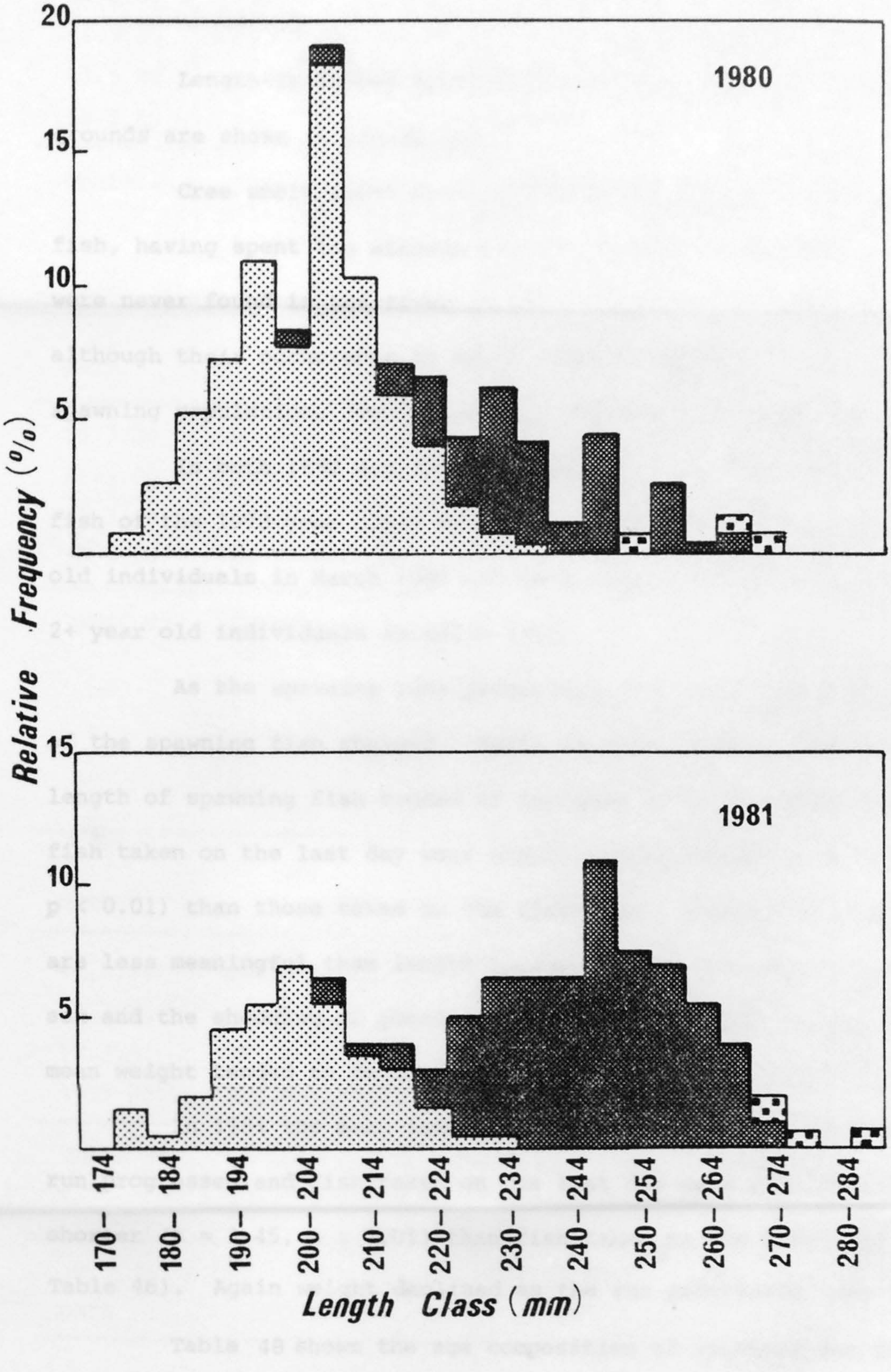


FIGURE 33: Length-frequency histograms for spawning run smelt from the river Cree, March 1980 and 1981 (1+ years old; 2+ years old; 3+ years old). Data refer to freshly measured lengths.

last two days of the run the numbers of fish present were greatly reduced in both years.

Length-frequency histograms for smelt sampled on the spawning grounds are shown in Figure 33.

Cree smelt first entered the spawning stock as 1+ year old fish, having spent two winters in the estuary. Immature 0-group fish were never found in the river in the vicinity of the spawning grounds although their occurrence in small numbers has been recorded from other spawning populations (eg. Lillelund, 1961; Ivanova and Polovkova, 1972).

In both 1980 and 1981 the spawning runs were dominated by fish of the 1978 year class which entered the spawning stock as 1+ year old individuals in March 1980 and were also numerically dominant as 2+ year old individuals in March 1981.

As the spawning runs progressed, the mean length and weight of the spawning fish changed. Table 44 shows that in 1980 the mean length of spawning fish tended to increase as the run progressed and fish taken on the last day were significantly longer ($t = 2.74$, $p < 0.01$) than those taken on the first day. Changes in mean weight are less meaningful than length because of the greater influence of sex and the shedding of gonadal products, but it can be seen that the mean weight tended to decline throughout the run. (See Table 45).

In 1981 the mean length of the fish tended to decline as the run progressed and fish taken on the last day were significantly shorter ($t = 3.45$, $p < 0.01$) than fish taken on the first day (see Table 46). Again weight declined as the run progressed (see Table 47).

Table 48 shows the age composition of spawning run fish and it can be seen that in 1980 the 1978 year class dominated the samples

DATE	ALL AGES	AGE (YEARS) 1+	2+	3+
10.3.80	210.1 ± 2.82	205.3 ± 2.24	235.8 ± 8.42	-
11.3.80	213.5 ± 7.95	204.1 ± 5.01	241.4 ± 18.30	-
13.3.80	211.7 ± 5.90	203.3 ± 3.47	233.3 ± 13.92	246.0
16.3.80	220.1 ± 6.70	204.0 ± 7.05	241.4 ± 6.06	256.6

TABLE 44: Changes in the mean length (mm) of spawning run smelt of all ages from the river Cree, March 1980. (± 95% confidence limits).

DATE	ALL AGES	AGE (YEARS) 1+	2+	3+
10.3.80	86.44 ± 4.11	80.13 ± 3.48	119.66 ± 12.42	-
11.3.80	84.51 ± 9.98	73.62 ± 6.89	117.66 ± 24.57	-
13.3.80	81.20 ± 7.53	71.31 ± 4.20	106.54 ± 20.80	124.50
16.3.80	85.37 ± 7.52	64.73 ± 4.27	111.97 ± 8.92	140.05

TABLE 45: Changes in the mean weight (g) of spawning run smelt of all ages from the river Cree, March 1980. (± 95% confidence limits).

DATE	ALL AGES	AGE (YEARS) 1+	2+	3+
10.3.81	236.8 ± 4.53	206.4 ± 4.68	247.3 ± 3.46	273.0
12.3.81	228.8 ± 4.75	200.6 ± 3.41	242.9 ± 3.70	279.0
13.3.81	223.9 ± 15.15	207.0 ± 11.04	259.4 ± 6.79	-
14.3.81	209.6 ± 16.47	185.7	231.0	-

TABLE 46: Changes in the mean length (mm) of spawning run smelt of all ages from the river Cree, March 1981. (± 95% confidence limits).

DATE	ALL AGES	AGE (YEARS) 1+	2+	3+
10.3.81	124.07 ± 7.19	80.25 ± 5.38	139.28 ± 6.39	212.90
12.3.81	103.25 ± 6.39	69.73 ± 4.07	118.47 ± 6.44	167.45
13.3.81	121.53 ± 24.12	93.94 ± 14.88	179.14 ± 8.72	-
14.3.81	81.19 ± 20.27	52.90	102.70	-

TABLE 47: Changes in the mean weight (g) of spawning run smelt of all ages from the river Cree, March 1981. (± 95% confidence limits).

	AGE (YEARS)		
	1+	2+	3+
1980:			
10.3.80	84.5	15.5	-
11.3.80	75.0	25.0	-
13.3.80	73.2	24.4	2.4
16.3.89	59.7	37.1	3.2
1981:			
10.3.81	29.3	69.5	1.2
12.3.81	35.6	62.5	1.9
13.3.81	58.3	41.7	-
14.3.81	75.0	25.0	-

TABLE 48: Age structure of spawning run smelt from the river Cree, March 1980 and 1981.

DATE	MALES		FEMALES		MALE:FEMALE	$X^2 - \frac{1}{2}$	P
	Abs.	Rel (%)	Abs.	Rel (%)			
(a) 1980							
10.03.80	67	46.2	78	53.8	0.86:1	0.69	$p > 0.05$
11.03.80	15	51.7	14	48.3	1.07:1	0.00	-
13.03.80	33	80.5	8	19.5	4.12:1	14.05	$p < 0.001$
16.03.80	53	84.1	10	15.9	5.30:1	28.00	$p < 0.001$
(b) 1981							
10.03.81	49	50.0	49	50.0	1:1	-	-
12.03.81	44	39.6	67	60.4	0.66:1	4.36	$p < 0.05$
13.03.81	13	86.7	2	13.3	6.5:1	6.66	$p < 0.01$
14.03.81	11	100.0	0	0	11.0:1	9.09	$p < 0.01$

TABLE 49: Changes in sex ratio of Cree smelt during the spawning runs in March 1980 and 1981.

		AGE (YEARS)		
		1+	2+	3+
1980	FEMALE	8.6	9.8	0
	MALE	3.9	2.6	0
1981	FEMALE	9.7	13.9	0
	MALE	6.7	0	0

TABLE 50: The proportion of immature smelt of all ages from the spawning runs into the river Cree in March 1980 and 1981.

TEMPERATURE (°C)	STAGE OF HATCH		
	1st	50%	100%
6	186 ± 8.0	219 ± 23.5	248 ± 11.0
10	150 ± 17.6	172 ± 14.0	212 ± 27.2
15	165 ± 17.0	172 ± 12.0	184.5 ± 19.9

TABLE 51: The sum of degree days to various stages of hatch at the three experimental temperatures in the egg incubation experiment.

(± 95% confidence limits).

on the first day (84.5%) but as the run progressed the proportion of 1+ year old fish declined, particularly between 13.03.80 and 16.03.80. At the same time, the proportion of 2+ and 3+ year old fish increased resulting in an increased mean length of fish.

In 1981, the 1978 year class again dominated the early stages of the run, this time as 2+ year old fish. As the run progressed however the proportion of these 2+ year old fish declined and the proportion of fish from the 1979 year class increased resulting in a decrease in mean length.

During the course of the spawning run marked changes also occurred in the sex ratio of spawning run fish (see Table 49). In both years, the early stages of the run were characterised by sex ratios close to unity. However, the later stages were dominated by male fish and in 1981 particularly it was extremely difficult to secure any female fish at all on the last day of the run.

In both 1980 and 1981 a proportion of the fish present on the spawning grounds were immature, details of which are shown in Table 50.

5:3:6 Duration Of The Egg Incubation Period

The relationship between the duration of the egg incubation period, expressed as time to first, 50% and 100% hatch, and water temperature is shown in Figure 34. The relationship was linear when plotted on logarithmic co-ordinates and was described by the regression equations:

First hatch $\log Y = -1.143 \log X + 2.362$ $r = 0.9870$ $p < 0.05$

50% hatch $\log Y = -1.269 \log X + 2.536$ $r = 0.9943$ $p < 0.001$

100% hatch $\log Y = -1.321 \log X + 2.645$ $r = 0.9999$ $p < 0.001$

The mean time taken for 50% hatch ranged from 11.5 days at 15° C to

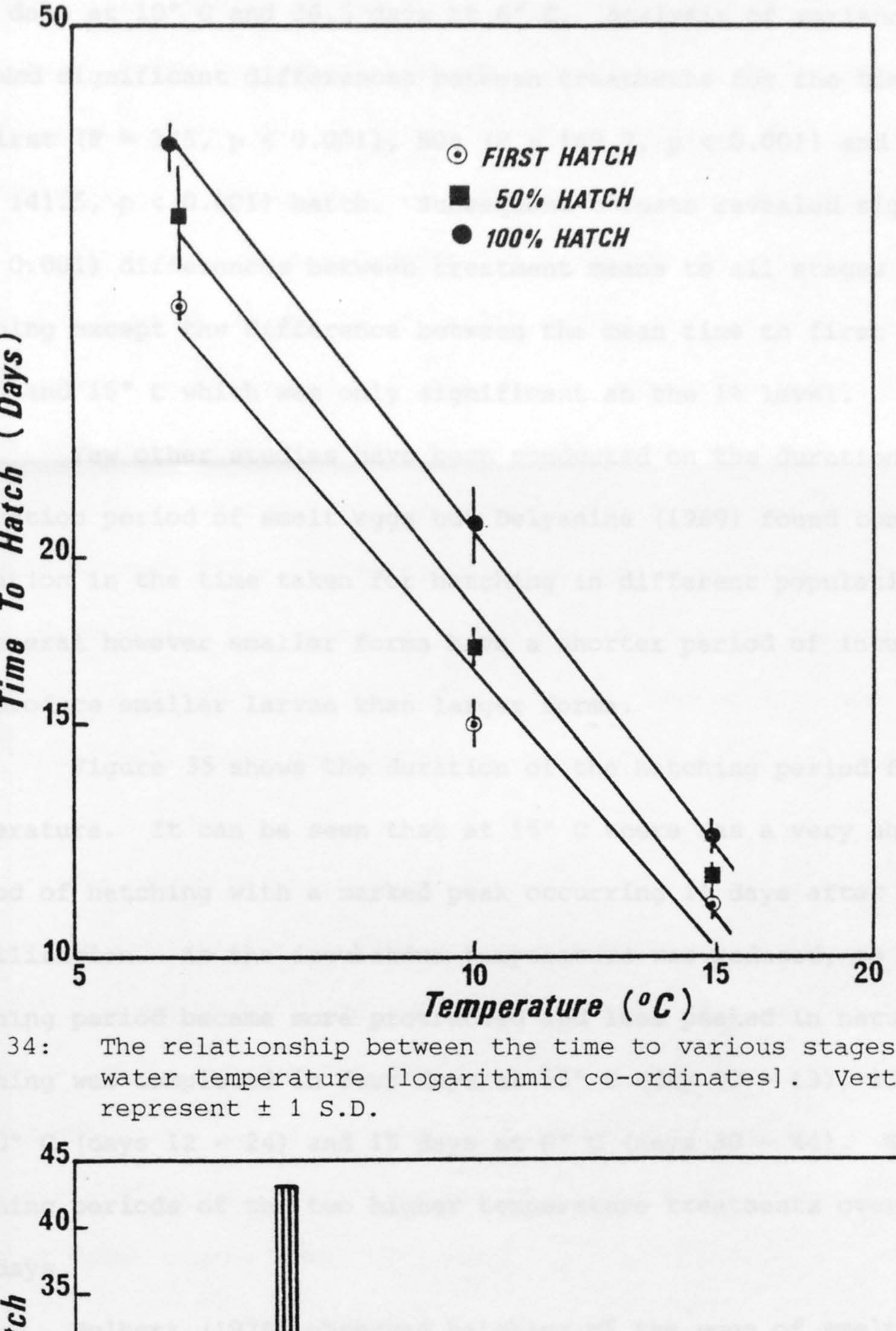


FIGURE 34: The relationship between the time to various stages of hatch and water temperature [logarithmic co-ordinates]. Vertical bars represent ± 1 S.D.

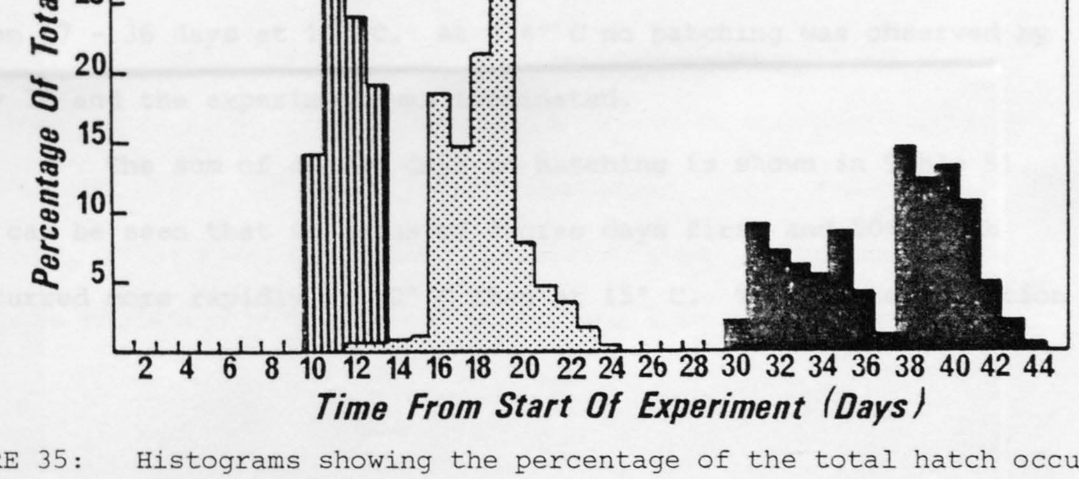


FIGURE 35: Histograms showing the percentage of the total hatch occurring on each day of the egg incubation experiment for each temperature regime (15°C; 10°C; 6°C).

17.2 days at 10° C and 36.5 days at 6° C. Analysis of variance revealed significant differences between treatments for the time taken to first ($F = 325$, $p < 0.001$), 50% ($F = 149.7$, $p < 0.001$) and 100% ($F = 141.5$, $p < 0.001$) hatch. Subsequent t-tests revealed significant ($p < 0.001$) differences between treatment means to all stages of hatching except the difference between the mean time to first hatch at 10 and 15° C which was only significant at the 1% level.

Few other studies have been conducted on the duration of the incubation period of smelt eggs but Belyanina (1969) found considerable variation in the time taken for hatching in different populations. In general however smaller forms have a shorter period of incubation and produce smaller larvae than larger forms.

Figure 35 shows the duration of the hatching period for each temperature. It can be seen that at 15° C there was a very short period of hatching with a marked peak occurring 11 days after fertilisation. As the incubation temperature was reduced, so the hatching period became more protracted and less peaked in nature. Thus, hatching was completed in four days at 15° C (day 10 - 13), 13 days at 10° C (days 12 - 24) and 15 days at 6° C (days 30 - 44). The hatching periods of the two higher temperature treatments overlapped by two days.

Hulbert (1974) observed hatching of the eggs of smelt, Osmerus mordax, from 19 - 55 days post fertilisation at 7.2° C and from 17 - 36 days at 10° C. At 4.4° C no hatching was observed by day 76 and the experiment was terminated.

The sum of degree days to hatching is shown in Table 51. It can be seen that in terms of degree days first and 50% hatch occurred more rapidly at 10° C than at 15° C. The shorter duration of the hatching period at 15° C resulted in the sum of degree days to total hatch being less than at 10° C. In contrast, Lillelund (1961) and Belyanina (1969) found the sum of degree days of the incubation period to increase exponentially with decreasing water temperatures.

The sum of degree days to 50% hatch varied from approximately 172 degree days at 10 and 15° C to 219 degree days at 6° C. Altukhov and Yerastova (1974) found that the incubation period lasted for 161 degree days but failed to state which temperature or to which stage of hatch this value referred. Hulbert (1974) found that hatching occurred between 137 - 396 degree days at 7.2° C and between 170 - 360 degree days at 10° C. McKenzie (1964) stated that the incubation period in the river Miramichi lasted for 174 degree days and Lillelund (1961) found that hatching occurred after 60 - 110 degree days.

The upper temperature tolerance of smelt eggs has been shown to increase from 17.7 - 20.7° C in the early stages of incubation, to 21 - 24° C prior to hatching (Lillelund, 1961). The results from Hulbert's (1974) experiments show that at temperatures less than 4.4° C the incubation period is extremely protracted although the experiment was terminated prior to hatching and it is not known if hatching would occur at temperatures lower than this.

5:4 DISCUSSION

The majority of investigators have shown that smelt, Osmerus spp., first enter the spawning stock as two year old fish (Ehrenbaum, 1909; Nordquist, 1910; Masterman, 1913; Van Oosten, 1940; Baldwin, 1950; McKenzie, 1958; Lillelund, 1961; Belyanina, 1969; Ivanova and Polovkova, 1972; Altukhov and Yerastova, 1974) and

	LENGTH GROUPS (mm)																			
	100	110	120	130	140	150	160	170	180	190	200	210	220	230	240	250	260	270	280	290
UCHINSKOYE WATERBODY	7.7																			
WHITE LAKE	4.6																			
RYBINSK WATERBODY	5.5			13.5																
KURISHES HAFF																				
PYAOSERO			2.9	5.8	6.4	15.1	20.1			45.6	48.5									
ONEGA LAKE	3.7	5.5	8.6																	
LADOGA LAKE	4.5	5.6	7.5	9.5	11.8	19.0	22.4	24.8	27.9	31.3	34.5	44.5	61.2							
KURISHES HAFF		5.3	7.8	11.2	16.1	17.0	19.7	24.4	26.1	31.3	36.7		41.9							
NEVA RIVER			10.9	12.2	13.6	16.1	16.1	25.4	30.8	35.0	33.9	41.5	45.2	45.5		68.5	93.5			
FINNISH GULF	5.3	6.4	9.8	12.7	16.7	19.5	23.6	31.9	33.6	41.9										
ELBE RIVER			6.5	8.0	12.0	14.5	18.0	22.5	28.0	35.0	38.0	45.0								
KANDALAKSHA BAY								30.1	32.9	35.8	49.6	61.4	72.0	80.5	83.5	114.0	124.0	137.0	140.0	161.0
ONEGA BAY				9.1	12.7	16.9	18.6	25.1	32.9		35.9	49.5	54.5	55.0	65.4	47.3				
GULF OF OB									15.5	16.3	22.8	25.0								
YENISEY RIVER														37.4	48.7	54.1				
RIVER CREE										32.4	36.2	38.6	42.9	-	77.9		106.0			
RIVER THAMES	5.8	8.3	10.9	14.2	16.9	15.4	26.2	23.9	37.6	48.6	27.2									

TABLE 52: The absolute fecundity of various populations of smelt, Osmerus eperlanus, (from Belyanina, 1969).

McKenzie (1958) considered that most smelt, on both sides of the north Atlantic, reach maturity at the end of their second year of life. Similarly, Belyanina (1969) found that most smelt populations reach maturity at 2 - 3 years of age but added that the age of maturity may differ widely in different populations. Smelt from the river Cree also first enter the spawning stock as two year old fish and mature 0-group specimens were never found. In contrast, Jensen (1949) and Belyanina (1969) found that many of the freshwater populations of smelt in northern Europe reached maturity in their first year of life and Jensen (1949) also found mature 0-group fish in some brackish water populations. In the river Thames only one mature 0-group smelt was identified from the 1980 year class, but the 1981 year class, which was characterised by improved growth rates, contained both mature male and female 0-group fish. Saunders and Power (1970b) also found that the more rapidly growing smelt attained sexual maturity earlier than the slower growing individuals. The results from the river Thames suggest that the attainment of sexual maturity by 0-group fish is dependent upon the males reaching a length of 100 - 109 mm and the females a length of 110 - 119 mm by the time of spawning. Unfortunately, it was not possible to determine if mature 0-group fish underwent the spawning migration typical of mature, older individuals.

Belyanina (1969) stated that some workers have noted that males reach maturity a year earlier than females, while others do not note such a difference. The results from both the Thames and the Cree show no evidence of earlier maturity in males although male 0-group smelt of the 1981 year class from the Thames reached maturity at smaller sizes than females. Similarly, Bailey (1964)(who found that all smelt, Osmerus mordax, less than 125 mm were immature) showed that while the shortest mature smelt was the same length for each sex, males were the first to reach 100% maturity. The data from the Thames suggest that age is also important in determining the minimum size at maturity since 1+ year old fish of the 1980 year class reached maturity at a smaller size than 0+ year old fish of the 1981 year class.

Studies of the smelt, Osmerus mordax, in North American waters have generally paid little attention to the fecundity of the species. Where fecundity estimates have been included (eg. Hoover, 1936; Baldwin, 1950; Bailey, 1964; Saunders and Power, 1970b) the data was limited and not subjected to detailed analysis. The largely inaccessible eastern Eruopean literature, which has included more rigorous studies of fecundity, has been summarised by Belyanina (1969) from which Table 52 has been abstracted and the results from the Thames and Cree incorporated. The data contained in Table 52 are not strictly comparable since no account is taken of different growth rates and hence age at a given size. Belyanina (1969) found that older fish produce more eggs than younger fish of the same size. The multiple regression analysis for the rivers Thames and Cree has shown however that age contributed insignificantly to the prediction of fecundity at both study sites.

Belyanina (1969) considered that landlocked freshwater smelt and Siberian populations possessed the lowest fecundities while migrant forms had the highest fecundities. Table 52 shows that in those lakes where the freshwater smelt grow to lengths comparable with the migrant forms eg. Ladoga Lake and Pyaosero Lake, the fecundity differs little from that of migrant smelt in the same size class.

Within the migrant populations listed in Table 52 there is reasonable similarity between the fecundities of any given size class. Notable exceptions are the high fecundities of smelt from Kandalaksha Bay and the low fecundities of smelt in the Gulf of Ob and the Yenisey river. The Kandalaksha Bay smelt population lives under conditions of higher salinities than other smelt populations and the food resources, particularly Nereis virens which is easily accessible and very abundant, are extremely rich (Abdel-Malek, 1966). Nikolsky (1962) emphasised the importance of fecundity changes in matching the size of the population to its resources, and Scott (1962) using rainbow trout, Salmo gairdneri, and Bagenal (1969) using brown trout, Salmo trutta, have shown experimentally that fecundity is higher in fish receiving larger rations.

Mann and Mills (1979) considered that since predation and starvation are the prime causes of larval mortality there are, within the optimal reproductive effort, two conflicting selection pressures. Increase in the number of eggs to overcome the effects of predation therefore conflicts with an increase in egg size to reduce larval starvation. Mann and Mills (1979) believed the result to be a compromise which is closely related to the conditions met by the newly hatched larvae. The data from this study have shown that Thames smelt exhibit high fecundity but small egg size while Cree smelt have fewer, larger eggs per gram of body weight.

Hermaphroditism has been reported more frequently in bony fishes than in any other group of vertebrates (Atz, 1964). However, outwith those species that are normally hermaphroditic the occurrence of hermaphroditic individuals is rare (Atz, 1964) and in the salmoniformes hermaphroditism has been reported infrequently. Where hermaphroditic salmonoids have been observed it has usually been as isolated examples obtained during large scale sampling operations eg. Scott (1975) recorded only one hermaphroditic powan, Coregonus lavaretus, from a total sample of 1000. Hutchinson (1983) has listed the species of salmonoids from which hermaphroditism has been recorded.

Unparalleled among the salmoniformes are Hoffmeister's (1939) observations on the smelt, Osmerus eperlanus, population of the river Elbe where 39 individuals from a total sample of 1019 fish were identified as abnormal hermaphrodites. The hermaphroditic individuals were mainly 1+ years old, with predominantly testicular ovotestes which were, in the main, at the same stage of ripeness as the gonads of gonochoristic individuals. Although eight of the ovotestes were predominantly ovarian, all the hermaphroditic specimens possessed nuptial tubercles (Hoffmeister, 1939). In contrast, all the hermaphroditic smelt from the river Thames that were identified during this study possessed predominantly ovarian ovotestes and nuptial tubercles were absent.

Lillelund (1961) also observed hermaphroditic smelt in the Elbe. He found that 1 - 2% of all adult smelt and 14% of all immature smelt of the 0-group were hermaphroditic, but he considered that many of the unripe hermaphrodites would develop into males at some later date. Jensen (1949) obtained only one hermaphroditic specimen from 769 Danish smelt and Hoffmeister (1939) failed to identify the condition from two other study sites. With the exception of an inaccessible paper in Russian (Podareva, 1967) no other records of hermaphroditism in smelt exist in the literature. Furthermore, the condition was not recorded from the river Cree despite the examination of a large number of mature specimens.

Atz (1964) concluded that since Hoffmeister (1939) had also obtained an unusually high proportion of hermaphroditic ruffe, Gymnocephalus cernua, from the river Elbe some environmental factor present in the river may have been responsible. The results from the river Thames show that under certain, as yet unidentified, conditions the normally gonochoristic smelt develops teratological hermaphroditism at a detectable level within the population.

Smith (1967) believed that some of the teratological hermaphrodites reported amongst gonochorists represent evolutionary experiments similar to those that have been successful in the past and have led to the fixation of hermaphroditism. However, despite much speculation the selective advantage of hermaphroditism remains a fundamental question (Smith, 1967).

Tomlinson (1966) considered that if the chances of encountering another animal were small then it would be highly advantageous to have a self-fertilising capacity. In this way, hermaphrodites are adapted to live in relative isolation or in small numbers either free-living or parasites eg. cestodes, gastropods, oligochaetes.

However, the majority of hermaphroditic fishes are either protogynous or protandrous and even in those that are synchronous hermaphrodites, some behave as gonochorists and undergo courtship and mating eg. Serranus subligarius (Smith, 1967). Other synchronous hermaphrodites do undergo self-fertilisation eg. Rivulus marmoratus (Harrington, 1963), but there is evidence that hermaphrodites which are forced to self-fertilise produce fewer viable embryos than when cross-fertilising (Heath, 1977). Heath (1977) therefore considered that in external fertilising hermaphrodites, where chances of self-fertilisation are high, simultaneous hermaphroditism should be rare.

Tomlinson (1966) showed that when individuals in a population are sparsely distributed, even if self-fertilisation is impossible there is a higher probability of at least one successful breeding contact between members of a hermaphroditic species. It is possible to speculate that in the initial phases of the recolonisation of the Thames tideway, smelt were a 'rare' species at West Thurrock until 1977 (Andrews, personal communication), there may have been an advantage in terms of breeding contacts in being hermaphroditic. However, Tomlinson's (1966) low density model was based on random encounters and the smelt is a gregarious species.

Altenberg (1934) suggested that simultaneous hermaphroditism would have a further advantage where an individual could afford to invest relatively little of its reproductive energy on male gametes. Where individuals mate rarely, the males may produce more sperm than they can profitably use in fertilising the ova of the few females that they encounter. Hermaphroditism would therefore increase the reproductive output. In some cases the number of ova may have to be reduced eg. when space in the brood cavity is limited and this would again favour hermaphroditism (Heath, 1977).

Heath (1977) showed that one of the costs of being hermaphroditic was that the energy available for gamete production by two hermaphrodites was less than the amount available to two gonochorists. The extent of this energetic disadvantage depends on the extent of the reproductive structures with the greatest disadvantage occurring when fertilisation is internal and the reproductive structures are complex. This energetic disadvantage can however be minimised by the utilisation of common membranes and ducts in hermaphrodites (Heath, 1977).

Despite the energetic disadvantage Heath (1977) considered the two main advantages of hermaphroditism were that reproductive contacts were more common at low density and the reproductive contacts can be made more profitable. Assuming both sets of hermaphroditic ova are fertilised the reproductive success will be higher.

It has been widely documented that the European smelt, Osmerus eperlanus, is a spring spawner but precise information regarding the timing of spawning runs in Britain is lacking. Pennant (1776) found that smelt spawned in March and April and noted that they never entered freshwater as long as snow melt water was present in the river. Cunningham (1896) considered the spawning season to be more protracted with spawning continuing into May and Masterman (1913) found that smelt populations of the Wash spawned in March and the contiguous weeks of February and April.

More precise information is available for smelt populations in America and continental Europe but there appears to be considerable geographical variation in the dates of the spawning runs. However, many workers have found an association between the commencement of the spawning run and the time of 'ice-out' (Kendall, 1927; Langlois, 1935; Hoover, 1936; Baldwin, 1950; Bigelow and Schroeder, 1953; Rupp, 1959; Rembiszewski, 1970; Ivanova and Polovkova, 1972; Scott and Crossman, 1973) although migrations under the ice have also been reported (Creaser, 1926; Rupp, 1959; Altukhov and Yerastova, 1974).

Altukhov and Yerastova (1974) found that the timing of the spawning runs fluctuated, commencing at the end of April in years when spring was early but being delayed until late May when spring was late. Van Oosten (1953) also identified considerable variation in the timing of spawning runs and stated that the migration was dependent upon water temperatures reaching >40° F (4.4° C) and possibly other factors. Other authors have also highlighted the importance of temperature in initiating the spawning runs. Thus initiation temperatures of 4 - 5° C in the main river and 6 - 7° C in the tributaries (McKenzie, 1964), 8 - 9° C (Scott and Crossman, 1973), 4.4 - 5.5° C (Bigelow and Schroeder, 1953), 4 - 6° C (Kuznetsov, 1974), > 4° C (Rembiszewski, 1970) and 2° C (Altukhov and Yerastova, 1974) have been reported. Belyanina (1969), after a thorough review of the eastern European literature, stated that "all over its range the smelt begins to spawn at water temperatures of > 4° C (sometimes ± 1 - 2° C) but with peak spawning occurring at 6 - 9° C".

In the river Cree, mid-afternoon temperatures were > 5° C in both years for which data were available. However, temperatures had exceeded 4° C for two weeks prior to the run in 1980 and for four days prior to the run in 1981 and it would therefore appear that factors other than temperature may also be operative.

Kendall (1927) believed that smelt were most eager in their ascent of rivers during violent gales of wind and snow, and in Denmark this habit has given rise to the term 'nors-il' or smelt squall. In contrast, Langlois (1935) found that warm days and cool nights created the optimum conditions for smelt runs. Banks (1969) has made a thorough review of the role of environmental variables in the migration of salmonids. While much of the information regarding meteorological variables is of interest, it should be remembered that much of what is discussed deals with 'homing to' the natal stream. Smelt being a truly estuarine species are not faced with the same problems of 'home stream' identity.

The most comprehensive study of the factors initiating smelt spawning migrations was carried out by Rupp (1959) who analysed data collected by wardens for 114 lake populations. He found a significant relationship between the time of most of the smelt runs and the time of 'ice-out' with a modal value occurring five days after 'ice-out'. However, he considered that there was no relationship between the time of the migrations and either calendar date or lunar cycle. Rupp (1959) also showed that there was a marked inconsistency in the timing of smelt runs with respect to temperature and spawning runs were witnessed at various temperatures (0 - 6.6° C) and spawning was even observed when anchor ice was forming. Rupp (1959) therefore considered that the release of spawning behaviour in smelt was due to a combination of factors and while he couldn't prove this he believed that the existence of a single mechanism operating to release spawning was unlikely. He therefore concluded that reproductive behaviour was released by cumulative action of heterogenous stimuli, a principle termed the 'law of heterogenous stimulus summation'. Fabricius (1950) showed that stimulus summation was responsible for the release of reproduction in pike, Esox lucius, char, Salvelinus alpinus, and whitefish, Coregonus spp.

McKenzie (1964) found that the duration of the spawning migration of smelt, Osmerus mordax, varied from stream to stream but in any one stream was much the same from year to year. In contrast, Hoover (1936) considered that the duration of the run was "somewhat dependent on temperature" and Belyanina (1969) found the spawning period to be protracted in colder years.

In the river Cree spawning lasted for approximately one week with the fish leaving the river in response to high flows for a period of 24 hours in both 1980 and 1981. Scott and Crossman (1973) reported that smelt are poor swimmers and personal observations during the spawning runs revealed that the fish exhibited considerable difficulty in holding their position during periods of high flows. However, discontinuities in the spawning runs may have been the result of population heterogeneity giving rise to temporally separated spawning peaks (Belyanina, 1969). Rupp (1959) also identified discontinuities in the spawning runs of Osmerus mordax and isolated storms, bright moonlight and interference by man as possible causes. In contrast, Rothschild's (1961) index of spawning intensity bore no relationship to environmental variables.

Belyanina (1969) stated that in most areas spawning of smelt, Osmerus eperlanus, lasted for approximately one month although peak spawning only lasted 2 - 4 days in most localities. Similarly, Rupp (1959), Scott and Crossman (1973) and Jilek et al (1979) found that while spawning could last for up to 3 - 4 weeks, the peak seldom lasted for more than one week. Spawning periods of 5 - 10 days (McKenzie, 1964), 8 - 10 days (Baldwin (1950), 3 - 4 weeks, (Pennant, 1776) and 8 weeks (Altukhov and Yerastova, 1974) have also been reported.

Belyanina (1969) stated that the majority of workers have noted a decrease in the size of smelt, Osmerus spp., during the spawning run with the older and larger individuals spawning first. McKenzie (1958) quantified this decrease in size and showed that the average length of smelt of 2, 3 and 4 years of age decreased by about 12.5 mm during the spawning season. Fish of 5 and 6 years of age showed an even greater decrease in length.

The changes in length during the spawning run in the river Cree can largely be accounted for in terms of the age structure of the spawners. In 1980, the 1978 year class which comprised recruits to the spawning stock was numerically dominant in the early stages of the run. In the later stages however, the proportion of 2+ and 3+ year old fish increased resulting in an increase in the mean length of the fish as the run progressed. In 1981, the reverse situation applied with the larger 1978 year class fish dominating the early stages of the run as 2+ years old fish and the proportion of the smaller 1+ years old fish increased as the run progressed. Bigelow and Welsh (1924) indicated that smelt associate in age groups at spawning time and Belyanina (1969) found that while autumn and winter concentrations consisted of both sexes and different age groups of smelt, the spring spawning aggregations consisted of grouping according to size and age.

Nikolsky (1963) considered that migratory smelt spawning populations consist of both recruits and residue but the numbers of the latter are small in comparison to the number of recruits. The results from the Cree together with Bailey's (1964) results provide evidence that the residue may be numerically dominant in the spawning runs. Bailey (1964) showed that an exceptionally strong year class three years previous, or a weak year class two years previous, could result in domination of the spawning runs by the residue. In the river Cree the strength of the 1978 year class and/or the weakness of the 1979 year class resulted in numerical dominance by residual fish during the 1981 spawning run.

Many workers have also observed changes in the sex ratio of spawning smelt as the spawning runs progress. The most frequently reported changes involve the early arrival of males on the spawning ground followed by the arrival of females, when a sex ratio of 1:1 or one that slightly favours the females prevails, followed by male dominance again in the later stages (Hoover, 1936; Lillelund, 1961; McKenzie, 1964; Belyanina, 1969; Ivanova and Polovkova, 1972; Altukhov and Yerastova, 1974). Belyanina (1969) found that female White sea smelt, <u>Osmerus eperlanus</u>, spawned for only a few hours and then dropped out of the river. Males in contrast continued to spawn with other females resulting in a shift in sex ratio towards male dominance. Bailey (1964) showed that spawning activity reached a peak when sex ratios approached unity.

The changes in sex ratio during the spawning runs in the Cree closely follow this pattern of change although there was no evidence that male smelt arrived on the spawning grounds first. Hoover (1936) believed that these changes in sex ratio could be of immense practical value since if exploitation could be restricted to the periods of male dominance the reproductive capacity of the species could be maintained without a complete ban on fishing. However, Greene (1930) believed that the fluctuations in the sex ratio, even during the course of a night, were such as to make a proper understanding of the changes extremely difficult.

In contrast to the studies described above Bailey (1964) found that males dominated the start of the spawning run, an approximately 1:1 ratio was present during the peak and females were more numerous towards the end of the run.

Hoover (1936) and Baldwin (1950) showed that spawning runs of landlocked smelt, *Osmerus mordax*, were characterised by entry into the stream after sundown followed by drift back into the lake during daylight. Only in heavily shaded sections of the streams, or on dull days (Langlois, 1935), did the fish remain in the river during daylight. These fish were invariably males and their number was estimated at less than 1% of the nights run. Van Oosten (1940) and Rupp (1959) also observed daytime presence of landlocked smelt but did not quantify the extent to which fish remained in the stream.

In the river Cree, smelt of both sexes were present in the river throughout the hours of daylight as also reported for marine smelt by Hoover (1936). However, there was evidence that the smelt dropped downstream from the areas of spawning and accumulated in areas of shade beneath the new A75 roadbridge or close into the heavily vegetated east bank of the river. It is possible that the energy expended in the migratory process may be responsible for this apparent difference between landlocked and estuarine populations. Baldwin (1950) found that landlocked smelt, *Osmerus mordax*, rarely travelled more than a quarter of a mile to spawn, while in the Cree the distance from Creetown Boathouse, where smelt were caught in all seasons, to the spawning ground is approximately 12 km. Although smelt remained in the river Cree throughout daylight spawning was never observed. Only on one occasion was a small group of approximately 25 smelt observed in the vicinity of the spawning grounds but the fish were merely holding position in a section of deep water out of the current. Rupp (1959) only observed daytime spawning in 2 out of the 114 lakes that he surveyed.

PLATES 11 & 12: Smelt in the Cree appear to exhibit a marked preference for spawning in the shallows.

Top: A group of spawning smelt left stranded by the receding tide.

Bottom: Reduced flow during the incubation period may result in considerable dessication of fertilised ova.

The spawning behaviour of smelt, Osmerus mordax, has been described in considerable detail by Hoover (1936), and to a lesser extent by Langlois (1935) and Lievense (1954). Prior to the work of Lievense (1954) and Rupp (1965) it was widely believed that smelt spawned only in running water. However, both of these authors identified shore spawning sites in the lentic environment.

In the river Cree, smelt do not ascend above the rapids located approximately 100 m upstream of the new A75 roadbridge and spawn in areas where salinities are low (see Table 5) but tidal influence is strong. Details of the composition of the substrate in this area that was found to contain spawn are shown in Appendix 3. Altukhov and Yerastova (1974) observed salinities in the range 0-2.4°/₀₀ on the spawning grounds of the White sea smelt. Lillelund (1961) found the upper salinity tolerance of smelt eggs to be dependent upon the state of embryological development, with stages prior to the formation of the embryo body being most sensitive. Upper salinity tolerances of 16°/₀₀ (Lillelund, 1961) and > 13°/₀₀ (Belyanina, 1969), have been reported. Unanyan and Soin (1963) (in Belyanina, 1969) showed that salinities of > 26°/₀₀ resulted in damage to the reproductive products and prevented fertilisation.

Wheeler (1971) indicated that Thames smelt spawn in the freshwater reaches below Teddington Weir. It is possible therefore that the proposed abstraction of freshwater from the Thames at Teddington Weir (Bulleid, personal communication) could have a marked effect on the spawning areas of the smelt since salinity changes are likely below the weir during abstraction.

Sexual dimorphism was marked in Cree smelt with males possessing clearly distinguishable nuptial tubercles or pearl organs and being darker in colour, particularly on the dorsal surface, than females. While nuptial tubercles are generally regarded as being a male secondary sexual character in smelt, Richardson (1942) provided evidence that females also undergo epidermal hypertrophy in minute patches although these can rarely be detected by touch or by the naked eye. Hoover (1936) considered that nuptial tubercles were of significance in mate selection. When two male smelt made contact prior to spawning they immediately separated whereas if a male came into contact with a non-tuberculated female he immediately drove her downwards or shoreward (Hoover, 1936). Observations made at night with a calor gas lamp during the spawning runs into the river Cree provided evidence of this shoreward thrust with fish frequently thrusting themselves clear of the water. Observations of the distribution of spawn the following day suggested a marked preference for spawning in the shallows, as also reported by Rembiszewski (1970), although this behaviour often resulted in large areas of spawn becoming dessicated when the tide, or river flow, receded. In this way, it seems likely that the hydrographic conditions prevailing during spawning and the subsequent incubation period could have a marked effect on year class strength.

Spawning smelt broadcast extremely adhesive eggs (Rothschild, 1961) the surrounding membrane of which becomes turned back after extrusion, remaining attached to the egg at one point (Norman, 1963). It is by this 'stalk' that the fertilised egg becomes attached to the substrate. Lillelund (1961) also believed that as the micropyle lay at the base of this funnel it may act as a channel for sperm.

Most authors have reported that the eggs of smelt develop while attached to the substrate and Unanyan and Soin (1963) found that only dead eggs became detached. Lillelund (1961) however believed that within a few days of spawning most of the eggs became dislodged and transported by water flow from the spawning grounds to the lower part of the river.

Rothschild (1961) found that the maximal prolarval production for smelt, Osmerus mordax, occurred at an egg density of 11745 eggs per square foot. The hatching success of landlocked smelt populations has been estimated at 0.55% of egg production in a stream (Rothschild, 1961) and from 0.027 - 2.096% for shore spawning in lakes (Rupp, 1965). Hulbert (1974) showed that eggs incubated on sand had a significantly lower hatching success than eggs incubated on two sizes of gravel.

Data derived from the egg incubation experiment showed that hatching prolarvae measure an average of 6.6 mm (5.5 - 8.0 mm) and exhibit a strong tendency to enter the water column immediately upon hatching. This behaviour is a result of a strongly positive phototactic response and aids the passive downstream migration of the larvae immediately after hatching (Belyanina, 1969).

Observations in the Cree estuary off Creetown Boathouse revealed large numbers of smelt prolarvae in the surface layers of the estuary on April 17th, 1982. At this time Eurytemora affinis was extremely abundant in the estuary and presumably provided an abundant 'first food' for the larvae. Ware (1977) showed that the peak hatching time of mackerel, Scomber scombrus, coincided with the time that zooplankton was most abundant.

CHAPTER 6: FOOD HABITS

6:1 INTRODUCTION

The study of diets based upon the analysis of stomach contents is now standard practice in fisheries ecology (Hyslop, 1980). Dietary studies are important in understanding the various aspects of the biology of fish, such as migrations, growth and seasonal variations in condition (Pillay, 1952), and for determining the status of various predatory and competing forms (Lagler, 1956).

Two major categories of dietary studies can be identified:

i) Studies which examine the diet of a fish population with a view to assessing the species' nutritional standing in the fish community

ii) Studies which attempt to estimate the total amount of food consumed by a fish population (Hyslop, 1980).

The majority of the available literature dealing with the diet of smelt, Osmerus spp., has been derived from studies in North American waters, particularly the Great Lakes. These studies have been concerned with assessing the smelt's nutritional standing with particular emphasis on its role as a predator on and/or competitor with the native species.

The early texts on British freshwater fishes stated that the diet of the smelt, Osmerus eperlanus, consisted of small fish, crustaceans (Day, 1884; Cunningham, 1896; Regan, 1911) and worms (Regan, 1911), and Wheeler (1969b) provided a comprehensive list of dietary components. However, none of these studies provided quantitative data and while Sedgwick (1979) provided numerical data regarding the diet of smelt in the Thames, the small sample size (n = 24) limited the conclusions that could be drawn.

While recent studies in North America have progressed to estimations of food consumption by smelt (Foltz and Norden, 1977a; Selgeby, MacCallum and Swedberg, 1978) there is a need for a thorough investigation of the nutritional standing of the smelt in Britain. The objectives of this chapter are to provide quantitative data on the diet of smelt and to examine any variations between seasons, size classes and study sites.

6:2 METHODOLOGY

A complete description of the methods of stomach contents analysis, including their respective advantages and disadvantages, can be found in the reviews of the subject by Hynes (1950), Pillay (1952), Lagler (1956), Windell and Bowen (1978) and Hyslop (1980).

Hynes (1950) considered that any of the commonly accepted methods of analysing stomach contents would give substantially the same result with important items in the diet being obvious irrespective of the method employed. More recent studies (eg. Windell and Bowen, 1978) have suggested that the suitability of the method of analysis will largely be determined by the nature of the study, but in general a combination of bulk and amount methodologies will present a more accurate picture of dietary importance (Hyslop, 1980). In this study, the data was analysed using a combination of occurrence, numerical and volumetric methods.

In the occurrence method, the number of stomachs that contained one or more individuals of each food category was expressed as a percentage of all the stomachs that contained food. The technique is quick and requires the minimum of apparatus (Hyslop, 1980) but it fails to indicate the numbers or bulk of the various food categories (Lagler, 1956).

Numerical analysis was used to express the number of individuals in each category as a percentage of the total number of individuals in all categories. This technique is also rapid and simple to use, and can be used to indicate the amount of effort exerted in selecting the prey (Ball, 1961). Hyslop (1980) considered that where the prey items are in the same size range, numerical analysis may be the most appropriate method. Where a range of prey sizes is encountered, however, numerical methods may overemphasise the importance of small prey items (Lagler, 1956).

Volumetric analysis was used to express the volume of each food category as a percentage of the total volume of all the stomach contents. Hyslop (1980) considered that volumetric analysis gave the best representative measure of bulk. Volume measurements also allow quantification of amorphous material although in this study this problem was rarely encountered since smelt are carnivorous and swallow their prey, which consists of discrete food units, without mastication.

While a combination of these three techniques was necessary to minimise the limitations and bias inherent in each method, interpretation of the results was complicated by the presence of three data sets. For this reason, an index of relative importance (IRI) (Pinkas, Oliphant and Iverson, 1971) combining percentage by number (%N), volume (%V), and frequency of occurrence (%F) was calculated using:

$$IRI = (\%N + \% V)\ \%F$$

This single value of dietary importance is useful when comparing diets using non-parametric ranking tests (Hyslop, 1980).

Using the above methods of analysis the diet of smelt was investigated using the procedure below.

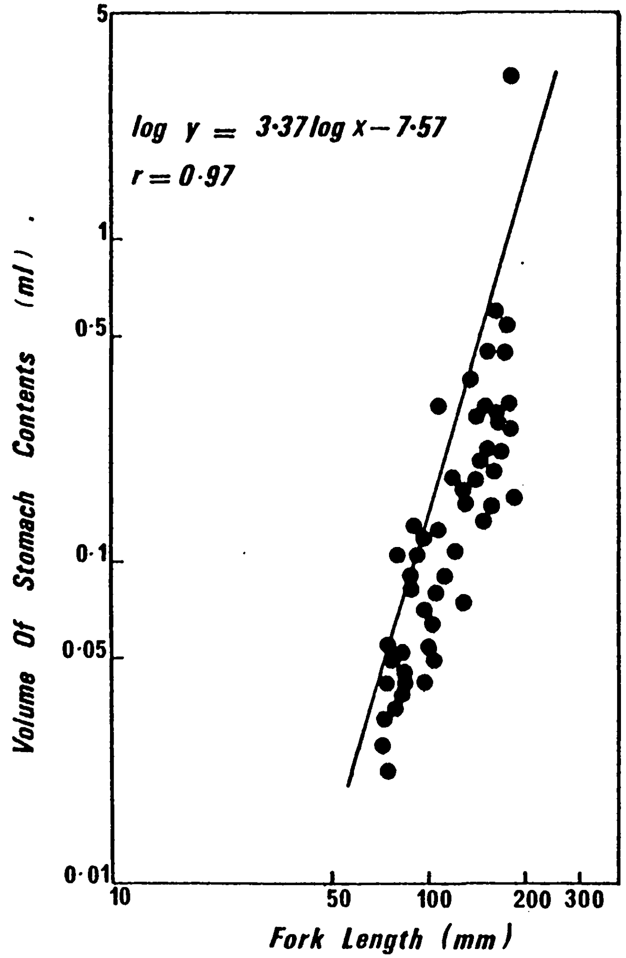


FIGURE 36: The relationship between the volume of stomach contents and fork length for Thames smelt [logarithmic co-ordinates] (see text for explanation).

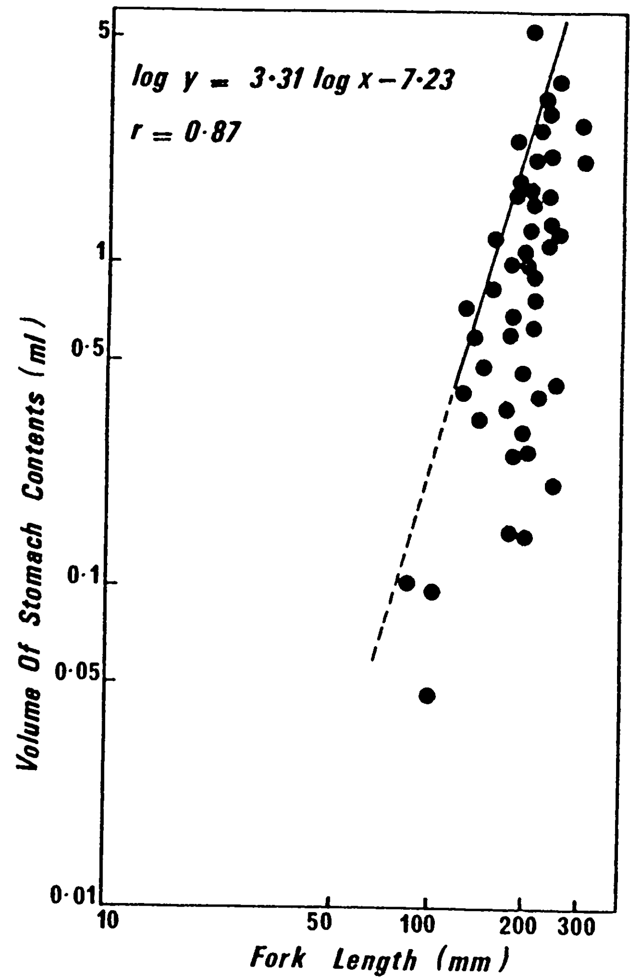


FIGURE 37: The relationship between the volume of stomach contents and fork length for Cree smelt [logarithmic co-ordinates].

The digestive tracts which had been dissected from the study fish and stored in numbered vials (Chapter 2), were transferred individually to a petri dish containing 70% ethanol. A subjective estimate of the state of fullness of each stomach was made by using Haram and Jones' (1971) modification of Ball's (1961) fullness scale. A non-subjective estimate of stomach fullness was made by using a modification of the graphical technique devised by Hellawell (1971). By plotting, on logarithmic co-ordinates, the volume of the contents of each stomach against the corresponding fish lengths and fitting a regression line to the outer most edge of the cluster of points (Figures 36, 37) an estimate of the maximum stomach capacity for each size of fish was obtained. By dividing the actual volume of the stomach contents of each fish by the corresponding maximum capacity a new measure of fullness, here termed the volumetric index, was calculated.

This new index was considered to be a more reliable indicator of seasonal feeding activity than the mean volume of the stomach contents, as used by Voigtlander and Wissing (1974), since the size of the fish is taken into account and any variation resulting from different size distributions of the fish in the samples is eliminated. Although the volumetric index has the advantage of being non-subjective, and is therefore reproducible, it suffers from the same drawbacks as other indices of feeding activity. These drawbacks stem from the fact that apparent seasonal variations may be due to different rates of digestion associated with changing water temperatures and/or the different digestibility of seasonally occurring prey (Hellawell, 1971)

Having determined the state of fullness of the stomach, its contents were removed using fine forceps. Identification and enumeration was restricted to organisms contained within the stomach, here delimited by a line extending from the base of the duodenal loop to the oesophagus, since digestion was less well advanced in this region. The contents were then identified, whenever possible to species level, and counted by viewing through a 'Nikon' binocular microscope using reflected light at magnifications ranging between X8 and X40.

The volume of each food category was determined for each stomach by one of two methods. In the case of large prey organisms, the surface alcohol was removed by blotting with absorbent paper and the volume was obtained by observing the displacement of water contained in a 10 ml graduated centrifuge tube. The volume of smaller organisms was determined by using the apparatus devised by Chubb (1961). This technique was favoured for small organisms since the presence of fine appendages may have hindered the removal of surface liquids resulting in errors in the volume displaced. The large surface area to volume ratio may have exacerbated such errors. The displacement method was adopted for larger organisms which could not be accommodated in the squash cell.

By adopting the squash technique, the volume of the stomach contents of the smallest smelt could be measured thereby eliminating the limitations of the work by Creaser (1928) and Lackey (1969) who concluded that the stomach contents of small smelt could not be measured volumetrically.

The comparability of the two methods of volumetric analysis was investigated using pieces of 'bluetak', the volume of which was determined first by displacement and then using the squash cell. Within the range of volumes that could be accommodated in the squash cell (< 0.700 ml) there was no significant difference between the two

MONTH	NO. STOMACHS EXAMINED	NO. CONTAINING FOOD Abs.	Rel(%)	NO. EMPTY Abs.	Rel(%)
FEBRUARY	50	26	52.0	24	48.0
MARCH	55	24	43.6	31	56.4
APRIL	73	27	37.0	46	63.0
MAY	*	*	*	*	*
JUNE	36	28	77.8	8	22.2
JULY	38	33	86.8	5	13.2
AUGUST	64	31	48.4	33	51.6
SEPTEMBER	39	22	56.4	17	43.6
OCTOBER	60	39	65.0	21	35.0
NOVEMBER	69	46	66.7	23	33.3
DECEMBER	69	52	75.4	17	24.6
JANUARY	52	37	71.2	15	28.8
FEBRUARY	34	25	73.5	9	26.5
MARCH	60	48	80.0	12	20.0
APRIL	60	48	80.0	12	20.0
MAY	40	34	85.0	6	15.0
	799	520	65.1	279	34.9

TABLE 53: The number of stomachs examined and the frequency of those that contained food and those that were empty on a monthly basis for smelt from the river Thames (* no samples).

SEASON	NO. STOMACHS EXAMINED	NO. CONTAINING FOOD Abs.	Rel(%)	NO. EMPTY Abs.	Rel(%)
AUTUMN	64	37	57.8	27	42.2
WINTER	71	12	16.9	59	83.1
SPRING	86	24	27.9	62	72.1
SUMMER	47	20	42.6	27	57.4
	268	93	34.7	175	65.3

TABLE 54: The number of stomachs examined and the frequency of those that contained food and those that were empty on a seasonal basis for smelt from the river Cree .

techniques ($t = 1.751$, $p > 0.05$).

Similarity of the diet as indicated by the different methods of analysis, between study sites and between size classes was investigated using the Spearman rank correlation coefficient (r_s) defined as:

$$r_s = 1 - \frac{6 . \sum di^2}{N^3 - N}$$

N = number of food categories
di = difference in rank for the i^{th} category

The primary advantage of this statistic is that it can be applied to the various types of percentage data commonly used in stomach contents analysis without prior transformation (Fritz, 1974). Despite this, it has been used infrequently in dietary studies, but where used (eg. Hellawell and Abel, 1971; Fritz, 1974) it allows an objective comparison of diets, or the methods used in dietary analysis, to be made.

Details of the number of stomachs examined and the frequency of empty stomachs are shown in Table 53 for the river Thames and Table 54 for the river Cree.

Data was also collected on the incidence of parasites within the digestive tract, the results of which are presented in Appendix 4.

6:3 RESULTS

6:3:1 Seasonal Variation In Feeding Activity

The seasonal pattern of feeding activity is shown in Figures 38, 39 and 40 for the river Thames, and Figures 41 and 42 for the river Cree.

It can be seen that the fullness index and the volumetric index show very similar seasonal trends. However, it should be noted

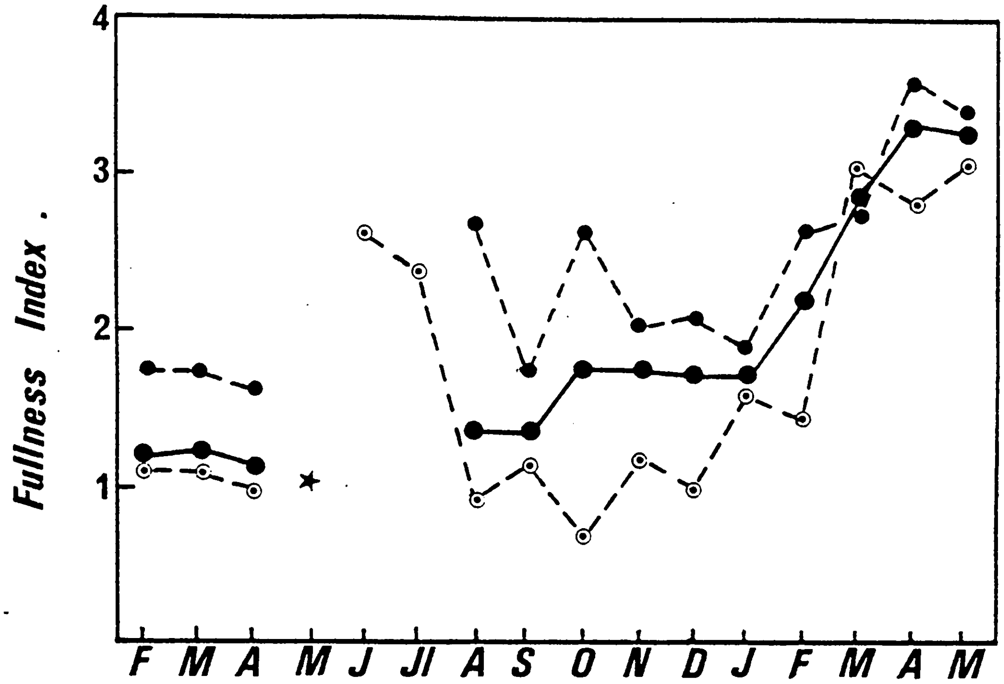


FIGURE 38: Seasonal variation in the feeding activity of Thames smelt as indicated by the mean fullness index (● 0+ years old; ⊙ > 0+ years old; ● age groups combined).

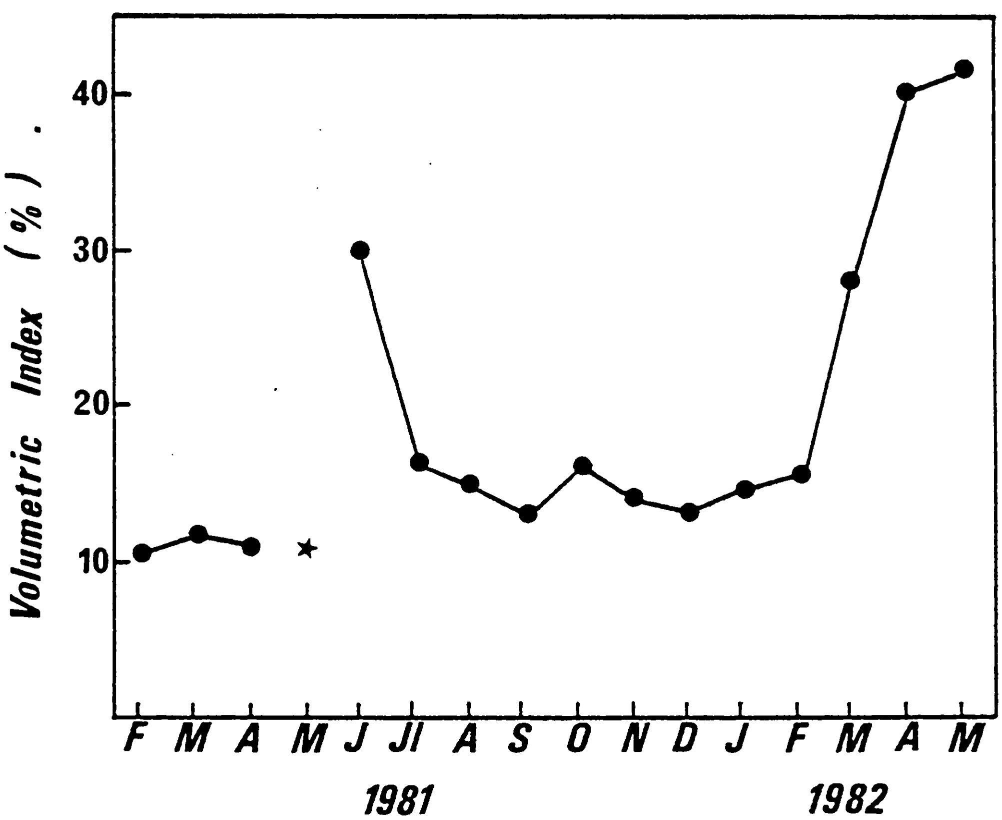


FIGURE 39: Seasonal variation in the feeding activity of Thames smelt as indicated by the mean volumetric index.

★no samples.

that the actual values derived from the two techniques differ. For example, in April 1982 the mean fullness index for Thames smelt had a value slightly greater than 3, which corresponds to a mean fullness of 75%. The corresponding mean volumetric index was approximately 40%. However, the usefullness of fullness scales lies in the assessment of comparative rather than absolute levels of feeding (Chubb, 1961).

Furthermore, the volumetric index was not entirely satisfactory since upon calculation some values were greater than 100%, as also reported by Hellawell (1971). Fortunately the number was low (4.4% and 2.1% of all samples containing food from the Thames and Cree respectively) and these were omitted from the results.

Although the volumetric index suffers from the drawbacks mentioned above it would appear that it presents a clear indication of seasonal variation in feeding activity which corresponds closely with the trends observed using the more traditional, subjective fullness index.

The values given in the text below refer to mean fullness index values with the corresponding mean volumetric index values given in parentheses.

Figures 38 and 39 show that in the river Thames, the period February to April 1981 was characterised by a low, constant level of feeding activity. No data are available for May 1981 but by June 1981 the activity had reached a peak with a doubling of the mean fullness index to 2.75 (30%). This peak of activity was followed by declining activity throughout the rest of the summer months resulting in a mean fullness index value of 1.4 (15%) in August and September 1981. There was an increase in feeding activity in October 1981, and from October 1981 until January 1982 a mean fullness index value of approximately

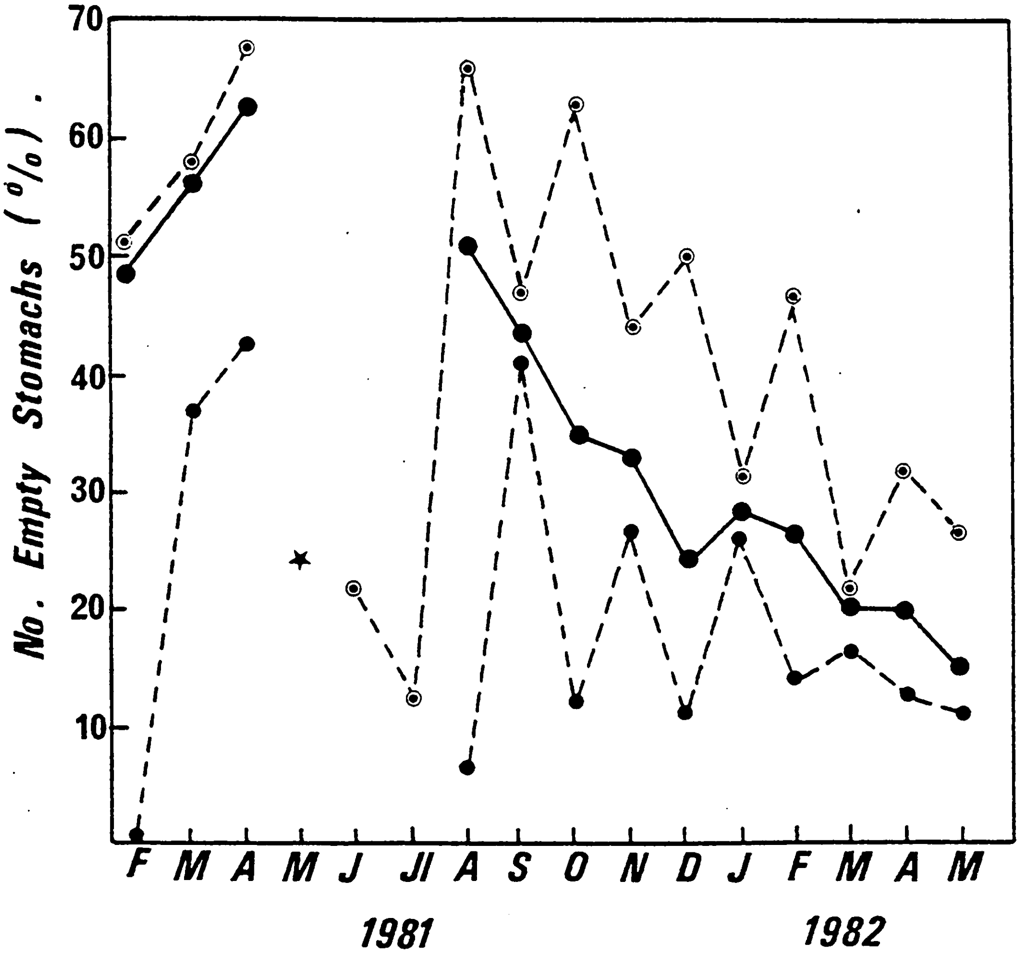
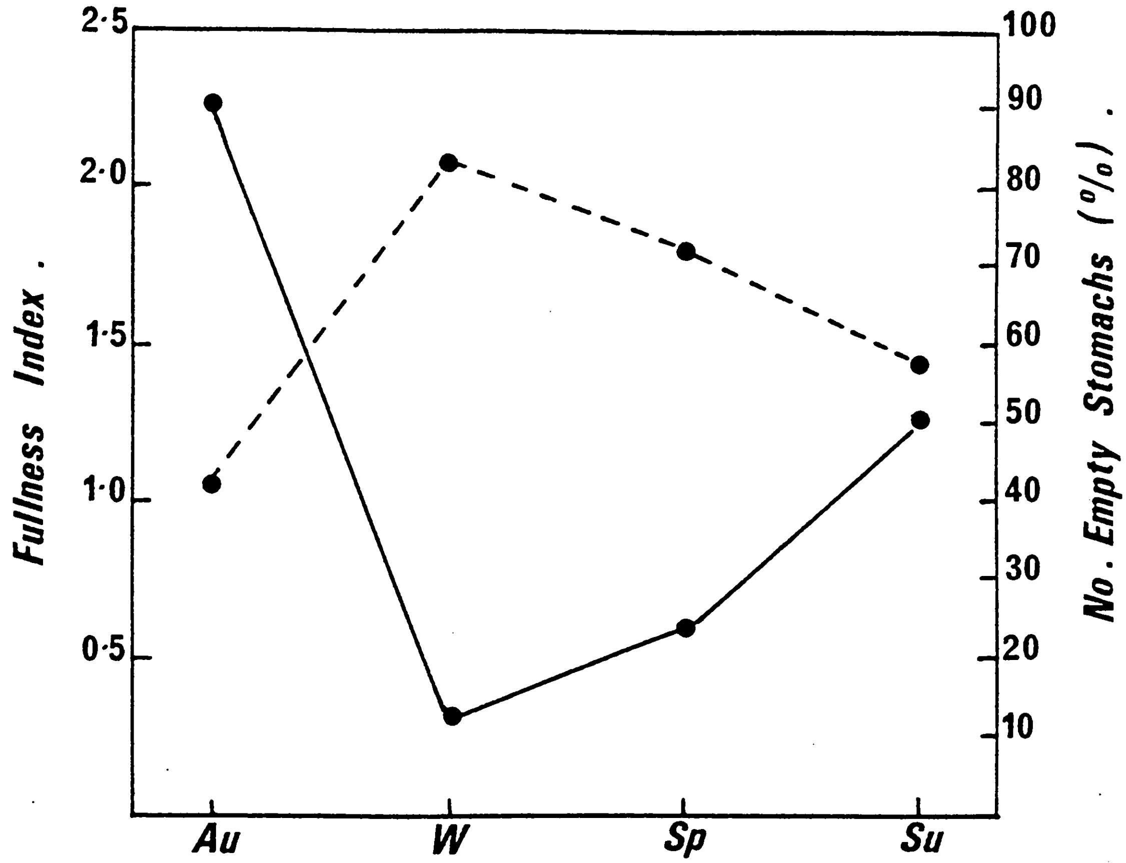


FIGURE 40: Seasonal variation in the feeding activity of Thames smelt as indicated by the proportion of stomachs containing no food. (● 0+ years old; ⊙ > 0+ years old; ● age groups combined).

★ no samples.

FIGURE 41: Seasonal variation in the feeding activity of Cree smelt as indicated by the mean fullness index (●—●) and the proportion of stomachs containing no food (●- -●).



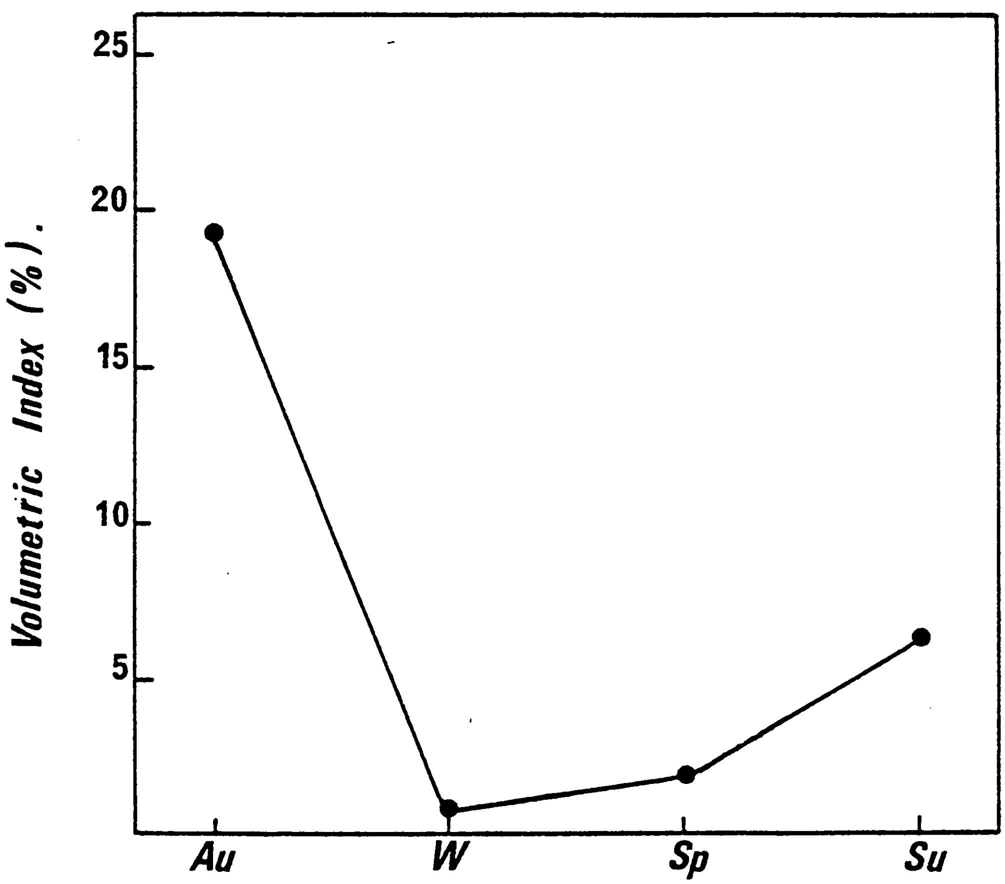


FIGURE 42: Seasonal variation in the feeding activity of Cree smelt as indicated by the mean volumetric index.

1.75 (13-16%) was maintained. The period from January to April 1982 was characterised by increased feeding activity which reached a peak in April 1982 with a mean fullness index of 3.2 (40%).

Figure 38 also shows that feeding activity was higher in 0-group fish than in the older age groups.

Figure 40 shows that the percentage of empty stomachs increased throughout the period February to April 1981 and reached a peak in April 1981 when over 60% of the stomachs analysed contained no food. By June 1981, the number of empty stomachs had declined and reached a low value of 12% in July 1981. In August 1981, 50% of the stomachs analysed contained no food but from August 1981 until May 1982 the dominant trend was for a steady decline in the percentage of empty stomachs. Figure 40 also indicates a higher level of feeding activity in 0-group fish.

Figures 41 and 42 present the data for the river Cree and it can be seen that feeding activity reached a peak value of 2.3 (19%) in Autumn and a low value of 0.3 (0.7%) in winter. There was a small increase in feeding activity in the spring and a continued increase in the summer. The percentage number of empty stomachs increased from 42% in autumn to a peak value of 82% in winter and then declined to 71% in spring and 55% in summer (see Figure 41).

Analysis of the stomach contents of spawning run fish failed to reveal any food organisms.

6:3:2 Composition Of The Diet

The composition of the diet of smelt from the river Thames is shown in Table 55.

	NUMBER Abs.	Rel(%)	OCCURRENCE Abs.	Rel(%)	VOLUME Abs.	Rel(%)	IRI
Neomysis integer	724	43.4	246	47.3	10.460	20.9	3041.4
Mesopodopsis slabberi	21	1.3	7	1.3	0.298	0.6	2.5
Unidentified mysids	17	1.0	14	2.7	0.090	0.2	3.2
Total mysids	762	45.7	265	51.0	10.848	21.7	3437.4
Gammarus zaddachi Gammarus salinus	791	47.5	224	43.1	26.971	53.8	4366.0
Crangon crangon	13	0.8	13	2.5	3.112	6.2	17.5
Sprattus sprattus	8	0.5	7	1.3	4.809	9.6	13.1
Gobiidae	17	1.0	16	3.1	3.615	7.2	25.4
Unidentified fish	4	0.2	3	0.6	1.116	2.2	1.4
Total fish	29	1.7	26	5.0	8.748	17.5	96.0
Corophium volutator	7	0.4	6	1.2	0.047	0.1	0.6
Fish eggs	8	0.5	2	0.4	0.007	0.1	0.2
Eurytemora affinis	58	3.5	3	0.6	0.016	<0.1	2.1
Unidentified material	-	-	20	3.8	0.338	0.7	-

TABLE 55: The composition of the diet of smelt from the river Thames as indicated by numerical, occurrence and volumetric methods, and by the index of relative importance (IRI).

The diet of Thames smelt was dominated by mysids and gammarids. The mysid component of the diet was represented by Neomysis integer and Mesopodopsis slabberi, although the latter species was only consumed by fish in the April 1982 sample. Praunus flexuosus, which also occurs in the estuary off West Thurrock (Andrews, personal communication) was never found to have been consumed by Thames smelt. Neomysis integer, the most common mysid in the Thames estuary (Andrews et al, 1982) occurred in more stomachs than any other organism but was less important numerically and volumetrically than the gammarids which were represented by Gammarus salinus and Gammarus zaddachi. So complete was the domination of the diet by mysids and gammarids that they each had an index of relative importance two orders of magnitude higher than the next most important food category.

Other fish species were also consumed by Thames smelt, particularly gobies. The transparent goby, Aphia minuta, occurred in one stomach but the dominant goby belonged to the genus Pomatoschistus and was probably the sand goby, Pomatoschistus minutus (Wheeler, personal communication). Sprats, Sprattus sprattus, were the only other identifiable fish species in the stomach contents.

Decapoda were represented in the diet by the brown shrimp, Crangon crangon. Corophium volutator, fish eggs and Eurytemora affinis were the only other organisms to be consumed. The appearance and size of the ova, and the date of their consumption, suggests that they may have been smelt eggs consumed during the spawning period. Eurytemora affinis was the third most important food category numerically but their small size and infrequent occurrence in the diet resulted in a relatively low IRI.

The small deviation of the sum of the percentage frequency of

	NUMBER		OCCURRENCE		VOLUME		IRI
	Abs.	Rel(%)	Abs.	Rel(%)	Abs.	Rel(%)	
Neomysis integer	28	12.0	18	19.3	0.764	1.5	260.5
Unidentified mysids	5	2.1	4	4.3	0.104	0.2	9.9
Total mysids	33	14.1	22	23.6	0.868	1.7	372.8
Gammarus zaddachi Gammarus salinus	24	10.3	18	19.4	0.778	1.5	212.4
Crangon crangon	35	15.0	27	29.0	10.491	20.0	1015.0
Clupea harengus	10	4.3	9	9.7	14.200	27.1	304.6
Osmerus eperlanus	24	10.3	23	24.7	23.100	45.9	1388.1
Gobiidae	3	1.3	2	2.2	1.100	2.1	7.5
Unidentified fish	3	1.3	3	3.3	0.530	1.0	7.4
Total fish	40	17.1	37	39.8	39.930	76.1	3709.4
Corophium volutator	12	5.1	8	8.6	0.286	0.5	48.2
Unidentified Cumacea	1	0.4	1	1.1	0.070	0.1	0.5
Eurytemora affinis	89	38.0	2	2.2	0.023	<0.1	83.9
Unidentified material	-	-	3	3.2	0.003	<0.1	-

TABLE 56: The composition of the diet of smelt from the river Cree as indicated by numerical, occurrence and volumetric methods, and by the index of relative importance (IRI).

occurrence values from 100% (actual value 108%) indicates that Thames smelt tend to concentrate on a given food category in any feeding bout. Stomachs rarely contained more than one food category thereby representing considerable specialisation.

The composition of the diet of smelt from the river Cree shown in Table 56 represented a shift away from the smaller organisms such as mysids and gammarids to larger food organisms such as fish and brown shrimp.

Fish, particularly underyearling smelt, was the dominant food category. Herring, *Clupea harengus*, and Pomatoschistine gobies were also consumed.

Brown shrimp, *Crangon crangon*, were consumed in larger numbers and occurred in more stomachs than any of the other major food organisms, but were considerably less important volumentrically, and consequently according to the IRI, than underyearling smelt.

Mysids, represented by *Neomysis integer*, and gammarids represented by *Gammarus salinus* and *Gammarus zaddachi* although numerous and frequent in occurrence were very much less important than the larger organisms volumetrically. As in the Thames, smelt from the Cree were never found to have consumed *Praunus flexuosus*, although this species was present in the estuary.

Eurytemora affinis and *Corophium volutator* were more important in the diet of Cree smelt than was the case in the Thames and one smelt from the Cree had consumed a cumacean which could not be identified. *Eurytemora affinis* was the most numerous single organism consumed.

The larger deviation of the percentage frequency of

FOOD CATEGORY	RANK THAMES	RANK CREE	di	di^2
MYSIDAE	2	3	+1	1
GAMMARIDAE	1	4	+3	9
CRANGONIDAE	4	2	-2	4
PISCES	3	1	-2	4
COROPHIDAE	6	6	0	0
FISH EGGS	7	8	+1	1
CUMACEA	8	7	-1	1
TEMORIDAE	5	5	0	0
				20
				$r_s = 0.762$
				$p < 0.05$

TABLE 57: Comparison of the diets of smelt from the rivers Thames and Cree. Food categories are ranked according to IRI.

FOOD CATEGORY	RANK NO.	RANK FREQ.	di	di^2	RANK NO.	RANK VOL.	di	di^2	RANK FREQ.	RANK VOL.	di	di^2
MYSIDAE	2	1	-1	1	2	2	0	0	1	2	+1	1
GAMMARIDAE	1	2	+1	1	1	1	0	0	2	1	-1	1
CRANGONIDAE	5	4	-1	1	5	4	-1	1	4	4	0	0
PISCES	4	3	-1	1	4	3	-1	1	3	3	0	0
COROPHIDAE	7	5	-2	4	7	6	-1	1	5	6	+1	1
FISH EGGS	6	7	+1	1	6	6	0	0	7	6	-1	1
TEMORIDAE	3	6	+3	9	3	6	+3	9	6	6	0	0
				18				12				4
				$r_s = 0.679$				$r_s = 0.786$				$r_s = 0.929$
				$p > 0.05$				$p < 0.05$				$p < 0.01$

TABLE 58: Comparison of the composition of the diet of Thames smelt as illustrated by the three methods of analysis. Food categories are ranked according to IRI.

FOOD CATEGORY	RANK NO.	RANK FREQ.	di	di^2	RANK NO.	RANK VOL.	di	di^2	RANK FREQ.	RANK VOL.	di	di^2
MYSIDAE	4	3	-1	1	4	3	-1	1	3	3	0	0
GAMMARIDAE	5	4	-1	1	5	4	-1	1	4	4	0	0
CRANGONIDAE	3	2	-1	1	3	2	-1	1	2	2	0	0
PISCES	2	1	-1	1	2	1	-1	1	1	1	0	0
COROPHIDAE	6	5	-1	1	6	5	-1	1	5	5	0	0
CUMACEA	7	7	0	0	7	6.5	-0.5	0.25	7	6.5	-0.5	0.25
TEMORIDAE	1	6	+5	25	1	6.5	+5.5	30.25	6	6.5	+0.5	0.25
				30				35.5				0.5
				$r_s = 0.464$				$r_s = 0.366$				$r_s = 0.991$
				$p > 0.05$				$p > 0.05$				$p < 0.01$

TABLE 59 : Comparison of the composition of the diet of Cree smelt as illustrated by the three methods of analysis. Food categories are ranked according to IRI.

occurrences from 100% (actual value 127%) indicates a slightly less selective mode of feeding in Cree smelt, and individual fish were often found to contain two or three food categories.

Indeterminate material was rarely encountered at either study site and the stomach contents were on the whole readily identifiable.

By ranking the food organisms according to their IRIs, a comparison of the relative composition of the diet from the Thames and the Cree was made using r_s. The results of this analysis are shown in Table 57, and it can be seen that the diets are significantly correlated ($r_s = 0.762$, $p < 0.05$).

The same statistic was applied to investigate the composition of the diet as illustrated by numerical, volumetric and frequency of occurrence methods. It can be seen that numerical and frequency of occurrence methods were not significantly correlated in either the Thames ($r_s = 0.679$, $p > 0.05$) or the Cree ($r_s = 0.464$, $p > 0.05$) (see Tables 58 & 59). Examination of the individual deviations (di and di^2) reveals that the elevated numerical rank of <u>Eurytemora affinis</u> is largely responsible for the low correlations. Comparison of the diet as illustrated by numerical and volumetric techniques also resulted in a low correlation in the case of the river Cree ($r_s = 0.336$, $p > 0.05$) but a significant correlation in the case of the river Thames ($r_s = 0.786$, $p < 0.05$). Comparison between frequency of occurrence and volumetric techniques resulted in significant correlations in both the Thames ($r_s = 0.929$, $p < 0.01$) and the Cree ($r_s = 0.991$, $p < 0.01$).

These results highlight the importance of adopting a combination of techniques for analysing stomach contents in order to achieve a representative picture of the diet.

6:3:3 Seasonal Variation In The Diet

The importance of mysids and gammarids in the diet of Thames smelt has been shown in Table 55. However, both of these food categories exhibit considerable seasonality in the diet of smelt as can be seen in Tables 60, 61, 62 and 63, and in Figure 43 which presents the frequency of occurrence data in graphical form.

Mysids were dominant in the diet during February (IRI = 15501) and March (IRI = 11468) 1981, but by April 1981 their importance had started to decline and reached a nadir in June 1981 (IRI = 71). Gammarids were absent from the diet in February 1981 but appeared in the diet in March 1981 (IRI = 74) and reached a peak of importance in June 1981 (IRI = 17324). Between June - September 1981 gammarids gradually declined in importance and were completely absent from the diet in October and November 1981. During the same period, mysids increased from the June low to a peak in December 1981 (IRI = 16319). Gammarids reappeared in small numbers in December 1981 and they dominated the diet from January - May 1982.

In April 1982 Mesopodopsis slabberi, a mysid that had not previously occurred in the diet, was consumed in addition to Neomysis integer.

Seasonality was less evident in the other food organisms because of their occurrence in relatively low numbers. Crangon crangon was present in the diet in February 1981 and 1982 and from July - December 1981 and they reached their peak importance in October 1981 (IRI = 582).

Fish were present in the diet of Thames smelt in all four seasons but they reached their peak importance in August 1981 (IRI = 1708) when all three categories of fish were present in the

FOOD ORGANISM	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY
Neomysis integer	95.2	93.8	30.8	*	3.5	36.0	78.6	86.5	95.7	98.3	96.6	48.1	-	-	2.2	-
Mesopodopsis slabberi	-	-	-	*	-	-	-	-	-	-	-	-	-	-	11.4	-
Unidentified mysids	-	-	-	*	-	5.6	4.1	-	-	-	-	7.6	-	0.7	-	-
TOTAL MYSIDS	95.2	93.8	30.8	*	3.5	41.6	82.7	86.5	95.7	98.3	96.6	55.7	-	0.7	13.6	-
Gammarus spp	-	2.7	56.9	*	95.7	50.6	6.1	3.8	-	-	2.6	44.3	86.7	56.0	86.5	99.3
Crangon crangon	1.6	-	-	*	-	1.1	2.0	1.9	3.4	0.8	0.9	-	3.3	-	-	-
Sprattus sprattus	3.2	-	-	*	-	-	3.1	-	-	-	-	-	3.3	1.4	-	-
Unidentified Gobiidae	-	2.7	-	*	-	4.5	3.1	7.7	0.9	0.8	-	-	-	-	-	0.3
Unidentified fish	-	-	-	*	-	-	3.1	-	-	-	-	-	-	0.7	-	-
TOTAL FISH	3.2	2.7	-	*	*	4.5	9.3	7.7	0.9	0.8	-	-	3.3	2.1	-	0.3
Corophium volutator	-	0.9	-	*	0.9	2.2	-	-	-	-	-	-	6.7	-	-	0.3
Fish eggs	-	-	12.3	*	-	-	-	-	-	-	-	-	-	-	-	-
Eurytemora affinis	-	-	-	*	-	-	-	-	-	-	-	-	-	41.1	-	-

FOOD ORGANISM	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY
Neomysis integer	66.1	51.0	25.6	*	1.5	26.4	23.6	23.9	54.1	79.1	87.8	29.9	-	-	1.1	-
Mesopodopsis slabberi	-	-	-	*	-	-	-	-	-	-	-	-	-	-	4.1	-
Unidentified mysids	-	-	-	*	-	0.8	1.6	-	-	-	-	1.9	-	0.1	-	-
TOTAL MYSIDS	66.1	51.0	25.6	*	1.5	27.2	25.2	23.9	54.1	79.1	87.8	31.8	-	0.1	5.2	-
Gammarus spp	-	3.2	74.0	*	98.3	57.4	7.3	1.6	-	-	5.9	67.7	48.9	58.0	94.8	97.9
Crangon crangon	-	-	-	*	-	1.7	10.4	48.1	42.1	12.7	6.3	-	10.8	-	-	-
Sprattus sprattus	13.8	-	-	*	-	-	19.9	-	-	-	-	-	36.2	38.7	-	-
Unidentified Gobiidae	-	45.7	-	*	-	12.0	16.2	22.4	3.8	8.2	-	-	-	-	-	1.0
Unidentified fish	-	-	-	*	-	-	20.8	-	-	-	-	-	-	2.4	-	-
TOTAL FISH	13.8	45.7	-	*	-	12.0	56.9	22.4	3.8	8.2	-	-	36.2	41.1	-	1.0
Corophium volutator	-	0.2	-	*	0.2	0.7	-	-	-	-	-	-	0.9	-	-	0.1
Fish eggs	-	-	0.4	*	-	-	-	-	-	-	-	-	-	-	-	-
Eurytemora affinis	-	-	-	*	-	-	-	-	-	-	-	-	-	0.2	-	-
Unidentified material	-	-	-	*	-	1.1	0.4	4.0	-	-	-	0.6	3.2	0.7	-	1.0

TABLE 60 (top): Seasonal variation in the composition of the diet of Thames smelt as indicated by numerical analysis.

TABLE 61 (bottom): Seasonal variation in the composition of the diet of Thames smelt as indicated by volumetric analysis.

FOOD ORGANISMS	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY
Neomysis integer	96.1	79.2	44.4	*	14.3	48.5	51.6	72.7	92.3	87.0	88.5	37.8	-	-	4.2	-
Mesopodopsis slabberi	-	-	-	*	-	-	-	-	-	-	-	-	-	-	14.6	-
Unidentified mysids	-	-	-	*	-	6.1	12.9	-	-	-	-	18.9	-	2.1	-	-
TOTAL MYSIDS	96.1	79.2	44.4	*	14.3	51.5	61.3	72.7	92.3	87.0	88.5	54.1	-	2.1	18.8	-
Gammarus spp	-	12.5	74.1	*	89.3	57.6	12.9	9.1	-	-	5.8	51.4	72.0	77.1	89.6	91.2
Crangon crangon	3.8	-	-	*	-	3.0	6.5	4.5	12.8	2.2	1.9	-	4.0	-	-	-
Sprattus sprattus	7.7	-	-	*	-	-	9.7	-	-	-	-	-	4.0	2.1	-	-
Unidentified Gobiidae	-	12.5	-	*	-	9.1	9.7	18.2	2.6	2.2	-	-	-	-	-	2.9
Unidentified fish	-	-	-	*	-	-	6.5	-	-	-	-	-	-	2.1	-	-
TOTAL FISH	7.7	12.5	-	*	-	9.1	25.8	18.2	2.6	2.2	-	-	4.0	4.2	-	2.9
Corophium volutator	-	4.2	-	*	3.6	6.1	-	-	-	-	-	-	8.0	-	-	-
Fish eggs	-	-	7.4	*	-	-	-	-	-	-	-	-	-	-	-	-
Eurytemora affinis	-	-	-	*	-	-	-	-	-	-	-	-	-	6.2	-	-
Unidentified material	-	-	-	*	-	6.7	10.5	4.2	-	-	-	2.5	21.4	12.2	-	5.7

FOOD ORGANISMS	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY
Neomysis integer	15501	11468	2504	*	71	3026	5273	8026	13826	15434	16319	2948	-	-	14	-
Mesopodopsis slabberi	-	-	-	*	-	-	-	-	-	-	-	-	-	-	226	-
Unidentified mysids	-	-	-	*	-	39	73	-	-	-	-	180	-	2	-	-
TOTAL MYSIDS	15501	11468	2504	*	71	3543	6614	8026	13826	15434	16319	4733	-	2	352	-
Gammarus spp	-	74	9700	*	17324	6221	173	49	-	-	49	5757	9763	8789	16244	17985
Crangon crangon	82	-	-	*	-	8	81	225	582	30	14	-	56	-	-	-
Sprattus sprattus	131	-	-	*	-	-	223	-	-	-	-	-	158	84	-	-
Unidentified Gobiidae	-	605	-	*	-	150	187	548	12	20	-	-	-	-	-	4
Unidentified fish	-	-	-	*	-	-	155	-	-	-	-	-	-	5	-	-
TOTAL FISH	131	605	-	*	-	150	1708	548	12	20	-	-	158	181	-	4
Corophium volutator	-	5	-	*	4	18	-	-	-	-	-	-	61	-	-	1
Fish eggs	-	-	94	*	-	-	-	-	-	-	-	-	-	-	-	-
Eurytemora affinis	-	-	-	*	-	-	-	-	-	-	-	-	-	256	-	-

TABLE 62 (top): Seasonal variation in the composition of the diet of Thames smelt as indicated by frequency of occurrence.

TABLE 63 (bottom): Seasonal variation in the composition of the diet of Thames smelt as indicated by the index of relative importance.

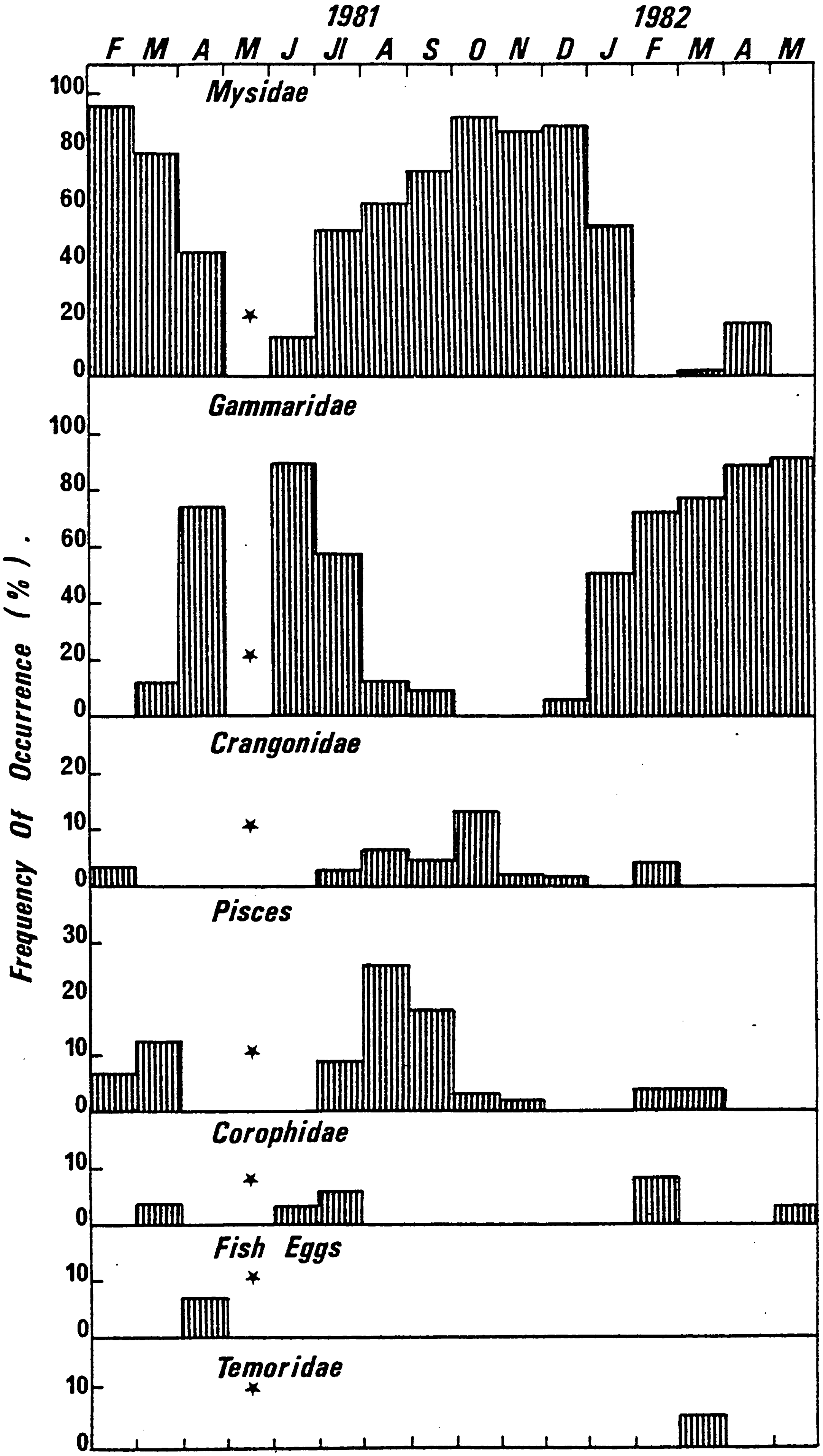


FIGURE 43: Seasonal variation in the diet of Thames smelt as indicated by frequency of occurrence data.

★no samples.

stomach contents.

Corophium volutator was only consumed between the months of February - July (peak importance in February 1982, IRI = 61) but was absent from the diet during late summer and autumn. Fish eggs were only found in the diet in April 1981 and Eurytemora affinis was only present in March 1982.

Data showing the seasonal variation in the diet of Cree smelt is presented in Table 64, and Figure 44 which presents the frequency of occurrence data in graphical form.

The major food categories (fish and brown shrimp) were consumed in all four seasons. However, consumption of underyearling smelt was dominant in the autumn (IRI = 3192) and summer (IRI = 2013) samples and outside these seasons only one underyearling smelt was consumed. Clupea harengus was consumed in all seasons except the summer and reached peak importance in winter (IRI = 1668).

Crangon crangon reached peak importance in autumn (IRI = 1537) but was important in all samples.

Mysids were relatively unimportant in the diet of Cree smelt in autumn (IRI = 3) and were absent from the diet in winter. Their importance increased in spring (IRI = 155) and they reached their peak importance in summer (IRI = 5159) when they were the most important single food category.

Gammarids were relatively unimportant in autumn (IRI = 13) and spring (IRI = 10) but they were the fourth most important food category in summer (IRI = 752) and they reached their peak importance in winter (IRI = 4537) when they were the single most important food category.

	AUTUMN				WINTER				SPRING				SUMMER			
	%N	%F	%V	IRI	%N	%F	%V	IRI	%N	%F	%V	IRI	%N	%F	%V	IRI
Neomysis integer	-	-	-	-	-	-	-	-	6.3	16.7	3.0	155	40.0	70.0	12.7	3689
Unidentified mysids	1.1	2.7	0.1	3	-	-	-	-	-	-	-	-	6.7	15.0	1.3	120
Total mysids	1.1	2.7	0.1	3	-	-	-	-	6.3	16.7	3.0	155	46.7	85.0	14.0	5159
Gammarus zaddachi *Gammarus salinus*	2.2	5.4	0.3	13	55.0	75.0	5.5	4537	1.6	4.2	0.9	10	16.7	35.0	4.8	752
Crangon crangon	22.0	35.1	21.8	1537	15.0	16.7	8.2	387	9.5	25.0	24.6	852	10.0	30.0	18.9	867
Clupea harengus	5.5	13.5	19.5	337	15.0	16.7	84.9	1668	3.2	8.3	33.8	307	-	-	-	-
Osmerus eperlanus	18.7	43.2	55.2	3192	-	-	-	-	1.6	4.2	23.6	106	10.0	30.0	57.1	2013
Unidentified Gobiidae	3.3	5.4	3.0	34	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified fish	-	-	-	-	-	-	-	-	4.8	12.5	13.4	227	-	-	-	-
Total fish	27.5	62.2	77.7	6543	15.0	16.7	84.9	1668	9.5	25.0	71.1	2015	10.0	30.0	57.1	2013
Corophium volutator	-	-	-	-	10.0	16.7	0.3	172	-	-	-	-	16.7	30.0	5.2	657
Unidentified Cumacea	-	-	-	-	5.0	8.3	1.0	50	-	-	-	-	-	-	-	-
Eurytemora affinis	47.2	2.7	<0.1	128	-	-	-	-	73.0	4.2	0.4	308	-	-	-	-
Unidentified material	-	-	-	-	-	-	-	-	-	-	-	-	-	15.0	<0.1	-

TABLE 64: Seasonal variation in the composition of the diet of Cree smelt as indicated by numerical, occurrence and volumetric methods, and by the index of relative importance (IRI).

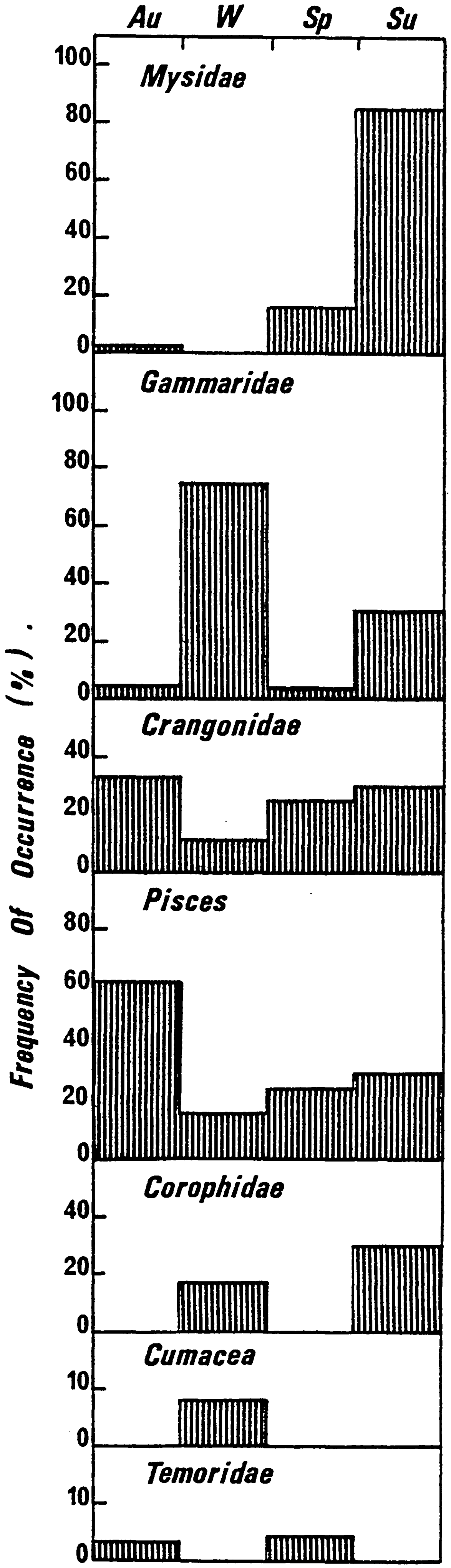


FIGURE 44: Seasonal variation in the diet of Cree smelt as indicated by frequency of occurrence data.

	SIZE CLASS (mm)											
	50 - 99				100 - 149				150 - 199			
FOOD ORGANISMS	%N	%F	%V	IRI	%N	%F	%V	IRI	%N	%F	%V	IRI
Neomysis integer	60.2	63.4	47.8	6847	39.8	49.2	21.9	3036	41.2	39.3	10.3	2023
Mesopodopsis slabberi	4.9	3.7	3.9	33	0.5	0.7	0.3	1	-	-	-	-
Unidentified mysids	0.9	0.7	0.1	1	0.7	2.0	0.3	2	0.3	1.8	<0.1	0
TOTAL MYSIDS	66.0	67.9	51.8	7999	41.0	49.8	22.5	3162	41.5	39.3	10.3	2036
Gammarus spp	24.6	31.3	45.6	2197	52.8	49.8	59.5	5592	52.4	58.9	43.3	5637
Crangon crangon	-	-	-	-	0.5	1.7	4.8	9	2.4	12.5	10.9	166
Sprattus sprattus	-	-	-	-	0.2	0.8	2.9	2	2.1	8.9	25.4	245
Unidentified Gobiidae	0.6	1.5	0.9	2	1.1	3.3	9.6	35	1.0	5.3	5.1	32
Unidentified fish	-	-	-	-	0.2	0.4	1.5	1	0.7	3.6	4.3	18
TOTAL FISH	0.6	1.5	0.9	2	1.5	4.5	14.0	70	3.8	17.9	34.8	691
Corophium volutator	0.3	0.7	0.6	1	0.5	1.7	<0.1	1	0.3	1.8	<0.1	0
Fish eggs	-	-	-	-	0.8	0.7	<0.1	1	-	-	-	-
Eurytemora affinis	8.5	1.5	0.1	13	2.9	0.3	<0.1	1	-	-	-	-
Unidentified material	-	4.0	1.0	-	-	3.5	0.8	-	-	2.7	0.6	-

TABLE 65: The composition of the diet of the three size classes of Thames smelt as indicated by numerical, occurrence and volumetric methods, and by the index of relative importance (IRI).

Corophium volutator was only present in the winter and spring and *Eurytemora affinis* only occurred in autumn and spring. The unidentified cumacean was only consumed by one smelt in the winter sample.

6:3:4 Variation In Diet With Size

Smelt from the river Thames were allocated to one of three size classes (50 - 99 mm; 100 - 149 mm and 150 - 199 mm) and variations in the diet were investigated. The results presented in Table 65 show that while mysids and gammarids were the dominant food organisms in all size groups, there were marked changes in diet with increasing size.

Mysids were the most important food organisms in the diet of the smallest size group (IRI = 7999) but their importance declined in the 100 - 149 mm (IRI = 3162) and the 150 - 199 mm (IRI = 2036) size classes.

Conversely, the importance of gammarids increased with size and they were the most important food category in the diet of both the 100 - 149 mm (IRI = 5592) and 150 - 199 mm (IRI = 5637) size groups. Similarly, brown shrimp, *Crangon crangon*, which was absent from the diet of the smallest smelt increased in importance with size, and other species of fish although consumed by all size groups were of peak importance in the diet of the largest smelt.

All other food categories were of minor importance in the diet. *Corophium volutator* occurred in the diet of all size groups but *Eurytemora affinis* was only consumed by the two smallest size groups. Fish eggs were only consumed by one individual from the 100 - 149 mm size group.

FOOD ORGANISMS	SIZE CLASS (mm) 100 - 199				200 - 299			
	%N	%F	%V	IRI	%N	%F	%V	IRI
<u>Neomysis integer</u>	12.1	30.6	2.8	456	11.6	10.0	0.6	122
Unidentified mysids	1.8	4.7	0.4	10	2.9	5.0	0.1	14
TOTAL MYSIDS	13.9	35.2	3.2	602	14.5	15.0	0.7	228
<u>Gammarus spp.</u>	6.7	18.9	2.0	164	18.8	22.5	1.3	452
<u>Crangon crangon</u>	9.7	32.9	17.1	882	27.5	30.0	21.5	1470
<u>Clupea harengus</u>	3.6	10.6	45.8	524	5.8	10.0	19.1	249
<u>Osmerus eperlanus</u>	3.0	12.9	21.1	311	27.5	42.5	56.5	3570
Unidentified Gobiidae	1.8	4.6	7.0	40	-	-	-	-
Unidentified fish	1.2	2.3	2.1	8	1.4	2.5	0.5	5
TOTAL FISH	9.7	32.9	75.9	2816	34.8	55.0	76.2	6105
<u>Corophium volutator</u>	6.1	9.6	1.6	74	2.9	7.5	0.1	22
Unidentified cumaceans	-	-	-	-	1.4	2.5	0.2	4
<u>Eurytemora affinis</u>	53.9	4.6	0.1	248	-	-	-	-
Unidentified material	-	-	-	-	-	7.5	<0.1	-

TABLE 67: The composition of the diet of the two size classes of Cree smelt as indicated by numerical, occurrence and volumetric methods, and by the index of relative importance (IRI).

FOOD CATEGORY	RANK 50-99	RANK 100-149	di	di^2	RANK 100-149	RANK 150-199	di	di^2	RANK 50-99	RANK 150-199	di	di^2
MYSIDAE	1	2	+1	1	2	2	0	0	1	2	+1	1
GAMMARIDAE	2	1	-1	1	1	1	0	0	2	1	-1	1
CRANGONIDAE	6.5	4	-2.5	6.25	4	4	0	0	6.5	4	-2.5	6.25
PISCES	4	3	-1	1	3	3	0	0	4	3	-1	1
COROPHIDAE	5	6	+1	1	6	5	-1	1	5	5	0	0
FISH EGGS	6.5	7	+0.5	0.25	7	6.5	-0.5	0.25	6.5	6.5	0	0
TEMORIDAE	3	5	+2	4	5	6.5	+1.5	2.25	3	6.5	+3.5	12.25
				14.5				3.5				21.5
			$r_s = 0.7411$				$r_s = 0.9375$				$r_s = 0.6161$	
			$p < 0.05$				$p < 0.01$				$p > 0.05$	

TABLE 66: Comparison of the composition of the diet of the three size classes of Thames smelt. Food categories are ranked according to IRI.

FOOD CATEGORY	RANK 100-199	RANK 200-299	di	di^2
MYSIDAE	3	4	+1	1
GAMMARIDAE	5	3	-2	4
CRANGONIDAE	2	2	0	0
PISCES	1	1	0	0
COROPHIDAE	6	5	-1	1
CUMACEA	7	6	-1	1
TEMORIDAE	4	7	+3	9
				16
			$r_s = 0.7143$	
			$p < 0.05$	

TABLE 68: Comparison of the composition of the diet of the two size classes of Cree smelt. Food categories are ranked according to IRI.

Table 66 shows the result of comparing the diets of the different size classes of Thames smelt using r_s. It can be seen that the diets of the 50 - 99 mm and 100 - 149 mm size classes are significantly correlated ($r_s = 0.741$, $p < 0.05$), and the diets of the 100 - 149 mm and 150 - 199 mm size classes are highly correlated ($r_s = 0.937$, $p < 0.01$). The diets of the 50 - 99 mm and 150 - 199 mm size classes were not however significantly correlated ($r_s = 0.616$, $p > 0.05$), largely as a result of the absence of Eurytemora affinis from the diet of the largest fish.

Smelt from the river Cree were allocated to one of two size groups (100 - 199 mm and 200 - 299 mm). The smaller number of fish containing food (n = 83) combined with the small number of fish less than 150 mm or greater than 250 mm prevented further sub-division but it was felt that these two classes would illustrate any gross shifts in diet with size. The results are presented in Table 67.

As was the case in the river Thames, the importance of mysids in the diet declined with increase in the size of Cree smelt. Gammarids, Crangon crangon and fish all increased in importance with increasing size. Corophium volutator was consumed by both size groups of smelt and Eurytemora affinis occurred only in the diet of the smaller size group.

The diets of both size classes of Cree smelt were significantly correlated ($r_s = 0.714$, $p < 0.05$) (see Table 68).

6:4 DISCUSSION

Many workers have drawn attention to the fact that smelt, Osmerus spp., cease feeding during the spawning period (Kendall, 1927;

Schneberger, 1936; Baldwin, 1950; Bigelow and Schroeder, 1953; Van Oosten, 1953; Nikolsky, 1856; Altukhov and Yerastova, 1974), and Nikolsky (1956) also found evidence of a pre-spawning fast. In contrast, Hoover (1936) found that male landlocked smelt, Osmerus mordax, fed throughout the spawning season including the day of spawning while spawning females did not feed.

The results from the river Cree show clear evidence of fasting during the spawning run and large numbers of non-feeding fish were also recorded in the samples taken one month prior to (18.02.82) and one month after (17.04.82) the start of the spawning run (11.03.82). It is not clear, however, whether this period of extended fasting is associated with the close proximity of the spawning run as suggested by Nikolsky (1956) or with conditions existing in the environment during winter and spring as suggested by Lackey (1969).

Belyanina (1966) (in Altukhov and Yerestova, 1974) found that well fattened smelt ceased feeding in the pre-spawning period while fish in poorer condition continued to feed. In the Cree however, there was no significant difference in condition between feeding and non-feeding smelt in the pre-spawning period ($t = 1.109$, $p > 0.1$).

The data from the river Thames showed no evidence of a pronounced spawning fast. A high proportion of adult fish ceased feeding in March and April 1981 (58% and 68% respectively) but there was no evidence of a spawning fast in March and April 1982 (only 20% of the stomachs examined were empty). It seems possible that this may be a sampling anomaly resulting from the different dates of collection of the April 1981 and 1982 samples (see Table 1). If the spawning fast in the Thames was short-lived the fish may have recommenced feeding by the time the April 1982 (26.4.82) sample was collected.

However, unlike the Cree population, the smelt of the river Thames showed no signs of a winter fast and it is possible that the artificially elevated temperatures in the middle reaches of the Thames estuary (Sedgwick, 1979) enabled the smelt to continue feeding throughout the winter months. Figure 2 shows that temperatures below 5°C were not recorded in the Thames estuary, off West Thurrock, during this study.

The large number of fish from the Thames that contained no food in their stomachs during August and September 1981 may also have been related to water temperatures. Peak temperatures of over 20°C were recorded in both these months (see Figure 2) and it is possible that such high temperatures inhibit the feeding of smelt as has been suggested for flounders, Platichthys flesus, by Moore and Moore (1976a) and demonstrated experimentally for cod, Gadus morhua, by Tyler (1970). Belyanina (1969) found that the feeding intensity of Osmerus eperlanus increased until July and then declined.

Figures 38 and 40 show that 0-group Thames smelt fed more intensively than the older age groups. Moore and Moore (1974, 1976a) found a similar trend and they showed that smaller flounders can catch their prey more efficiently than larger specimens. Moriarty (1978) also drew attention to the decreased prey capture efficiency in larger eels, Anguilla anguilla, which underwent periods of starvation as a result of the difficulties involved in securing fish prey.
Moore and Moore (1974) showed that the decreased feeding intensity in large char, Salvelinus alpinus, was a reflection of decreasing metabolic rate with increasing size. It seems reasonable to assume that similar mechanisms are operative in Thames smelt and that either

a decreased metabolic rate and/or a change of diet to larger organisms with more efficient "escape reactions", especially in turbid estuarine waters, is responsible for the lower feeding intensity of the larger Thames smelt.

Foltz and Norden (1977b) showed that smelt, Osmerus mordax, commenced feeding after dusk with maximum feeding intensity between 1600 - 2400 hours, corresponding with the vertical migration of Mysis relicta. Similarly, Amstislavsky and Brussynina (1963) found that the period of peak feeding activity of Osmerus eperlanus corresponded with the vertical migration of zooplankton but found evidence of both diurnal and nocturnal feeding.

No attempt was made to assess feeding chronology during this study with all the samples being collected during daylight. In most cases however, the stomach contents were readily identifiable and showed no evidence of extended periods of digestion. Unidentifiable material, which when present occurred in small quantities, exhibited a bimodal distribution, occurring most frequently in mid-summer and late winter. Burbidge (1969) attributed an increased quantity of 'remains' during winter months to an increased retention time of food in stomachs at low temperatures, while the summer peak is probably a result of increased rates of digestion at higher temperatures (Tyler, 1970).

The undigested state of most of the organisms indicates that either the sampling periods coincided closely with periods of feeding or that digestion rates in smelt are low. Day (1884) quotes the results of the experiments of a Mr. W. Wankly who found that the rate of digestion was so great that while most smelt stomachs that were examined fresh contained identifiable food, by the time the fish were taken home only digested remains were to be found. Furthermore, when the unfortunate Mr. Wankly blew his nose on a hankerchief previously used to remove the gastric juice from his hands, "both his nostrils and lips were inflamed and irritated and more than once his tongue swelled in an extraordinary manner" (Day, 1884). This inflamation was attributed to the 'acrid nature' of the smelts digestive juice. MacMahon (1946) also drew attention to the rapidity of the smelt's digestive processes.

If such rapid post-mortem digestion rates occur in living smelt, then a difference in sampling time of a few hours could introduce apparent variations in the seasonal pattern of feeding intensity. While the time of sampling varied considerably through the hours of daylight, the samples were always collected on a rising tide and the lack of extended digestion may be indicative of a tidal rather than diurnal/nocturnal pattern of feeding. The presence of tidal rhythms in shallow water marine organisms has been reported by Palmer (1974) and Gibson (1978), and synchronisation of feeding with the tidal cycle has been demonstrated in the sand goby, Pomatoschistus minutus, by Healey (1971) and Gibson and Hesthagen (1981), and in flounders, Platichthys flesus, by Gibson (1978). Tidally synchronised feeding was however absent in fish populations of the Severn estuary (Moore and Moore, 1976a, 1976b).

Smelt, Osmerus spp., have been variously described as gregarious and voracious (Day, 1884); voracious fish of prey (Smitt, 1895); greedy fish of prey (Regan, 1911); rapacious feeders (Jensen, 1949); versatile feeders (Gordon, 1961) and miniature predators (Nilsson, 1979). While the ferocious dentition and agile, streamlined body provide clear evidence of a predatory existence (Smitt, 1895; Nilsson, 1979) conflicting opinions exist regarding the location of the feeding station of smelt within the water column. Rembiszewski (1970) found that smelt, Osmerus eperlanus, could dig their food out of the bottom mud but Burbidge (1969) found no evidence of bottom feeding by Osmerus mordax. Nilsson (1979) provided evidence of both benthic and pelagic feeding activity and the results of dietary analysis from other studies also suggest both types of feeding.

The composition of the diet from the rivers Thames and Cree includes both benthic and pelagic species. However, in the Thames estuary at least, the tidal currents are sufficiently strong to cause gammarids, and presumably other benthic organisms, to appear in the water column, as witnessed by their occurrence in plankton tows (Huddart and Arthur, 1971a). Furthermore, water movements and turbulence in power station screenwells brings unusual species, such as polychaetes, into the water column thus making them available as food items (Turnpenny et al, 1981). The possibility of a totally pelagic mode of feeding cannot therefore be eliminated. There was no evidence that the smelt from either study site had dug food organisms from the substrate. The only member of the infauna to be consumed was the amphipod Corophium volutator, but the absence of bottom sediment from the stomach contents indicates that smelt only feed on this organism when they emerge from their burrows (McLusky, 1981) and possibly only if they appear in the water column. This implies that the considerable infaunal estuarine resources (eg. Neanthes diversicolor may achieve densities of 3000 m^{-2} at Greenhithe (Andrews et al, 1982)) are inaccessible to smelt.

The diet of Thames and Cree smelt comprised four major food categories - viz. Mysidae, Gammaridae, Crangonidae and various fish species. The other food categories viz. Temoridae, Cumacea, Corophidae and fish eggs were very much less important in the diet. Although the relative contribution of each category varied between each study site, qualitatively the diets were significantly correlated.

Nikolsky (1963) divided the diet of fish into three categories according to the importance of respective food organisms. Using this system of classification and applying it to the diet of Thames smelt, Neomysis integer and Gammarus spp., would be regarded as basic food; fish (Gobiidae and Sprattus sprattus) and Crangon crangon would be secondary food items and all other categories would be regarded as incidental. In the case of Cree smelt, fish (underyearling smelt, Clupea harengus and Gobiidae) and Crangon crangon would be basic foods; Neomysis integer and Gammarus spp., would be secondary food items and all other categories would be incidental. However, this classification takes no account of size class variations in diet and while being useful for comparing the diets of different populations of the same species, or of different species in the same environment, to present a detailed picture of the diet it should be applied to individual size groups.

The composition of the diet for Thames and Cree smelt corresponds closely with the literature for other estuarine populations of smelt.

Pirojnikov (1955) found that Lena river smelt, Osmerus eperlanus, fed on amphipoda, mysidaceae, copepoda, cladocera and young of the year smelt, and the same components made up the diet of Ob river smelt

(Amstislavsky and Brussynina, 1963). In the Elbe river, Ladiges (1935) (in Belyanina, 1969) found that Eurytemora spp. and Gammaridae were the main food items while in Danish waters smelt fed on fish (often underyearling smelt), fish eggs, Neomysis vulgaris, Gammarus spp. and Crangon spp. (Jensen, 1949).

The results of the present study are in close agreement both with the studies listed above and with the dietary list provided by Wheeler (1969b) which included sprats, herring, gobies, young gadoids, brown shrimp, Gammarus spp., Corophium spp., isopods and copepods. Jensen (1949) concluded that:

> "German and Finish authors have made a number of investigations leading to quite the same results so that we must be said to be well informed with regard to this side of the biology of the smelt."

Belyanina (1969) supported this statement by adding that

> "the main food groups of adults of different populations are Mysidaceae, Amphipoda and young fish."

While the results listed above indicate that estuarine smelt populations tend towards stenophagy, Kuddersky and Russanova (1963) (in Belyanina, 1969) listed more than 60 components in the diet of White sea smelt, Osmerus eperlanus, with polychaetes being the dominant food category. A more euryphagic diet was also reported by Bigelow and Schroeder (1953) who found that the diet of smelt, Osmerus mordax, consisted of decapods, mysids, gammarids and small fish but also included shellfish, squid, polychaetes and crabs.

It seems likely that availability is the dominant factor in governing the stenophagic nature of the diet of smelt in brackish waters since estuaries are characterised by low diversity and high abundance (McLusky, 1981). However, the accessibility of the prey and the food preferences of smelt probably also contribute to the

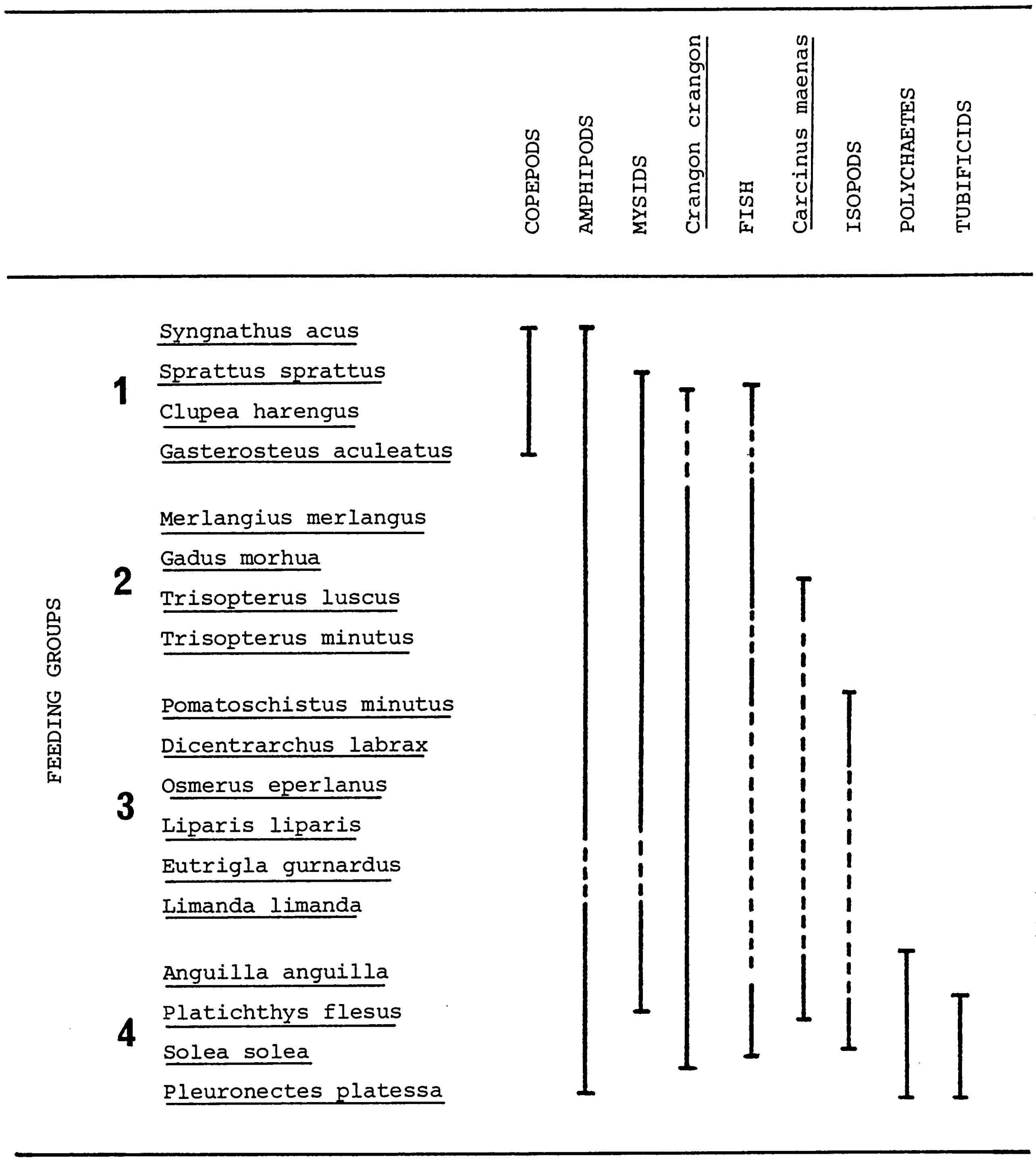


FIGURE 45: Feeding groups of fish species in the estuary of the river Thames (from Sedgwick, 1979).

limited list of dietary components.

The only other quantitative study of the diet of smelt, Osmerus eperlanus, in Britain was carried out by Sedgwick (1979). He found that the diet of Thames smelt consisted entirely of crustacean epifauna, with a marked preference for mysids. Other prey included Crangon crangon and Gammarus salinus but not isopods or Corophium volutator. The absence of Gammarus zaddachi from the diet of smelt in Sedgwick's (1979) study (which was based on samples from both CEGB West Thurrock and CEGB Tilbury) can be explained by the fact that all the smelt collected that contained gammarids came from CEGB Tilbury, some 8 km downstream of West Thurrock, and in a salinity zone of the estuary where Gammarus salinus is the only gammarid present.

Sedgwick (1979) suggested several groupings for Thames fish based on the similarity of their diets (reproduced with permission from Dr. Sedgwick as Figure 45) and concluded that the differences in food spectra and the ability to adapt their diets enabled the fish species to avoid mutual exclusion. Only within Group 3 was the degree of similarity of the diet indicative of some interaction, although since the members of this group were feeding on the most abundant prey, the conflict may have been more apparent than real (Sedgwick, 1979). The results of this study have made several additions to the dietary list of Thames smelt, notably the inclusion of other species of fish. On the basis of these results, Group 2 would appear to be a more appropriate feeding group for smelt.

A number of studies have also been carried out on the diet of landlocked smelt populations, the results of which are shown in Table 69.

AUTHORITY	CLADOCERA	COPEPODA	OSTRACODA	MYSIDACEA	AMPHIPODA	ISOPODA	DIPTERA	EPHEMEROPTERA	MOLLUSCA	TRICHOPTERA	HEMIPTERA	FISH	INSECTA	ALGAE	ODONATA	FISH EGGS
KENDALL (1926)	*	*										*				
CREASER (1928)		*										*				
GREEN (1930)	*	*										*		*		
SCHNEBERGER (1936)				*	*		*	*	*			*				
JENSEN (1948)	*	*										*				
BALDWIN (1950)			*	*			*	*				*				
GORDON (1961)	*	*	*		*			*				*		*		
BELYANINA (1969)	*	*		*	*							*				
BURBIDGE (1969)	*	*	*	*	*		*					*				
LACKEY (1969)	*	*				*							*			
ANDERSON & SMITH (1971)	*	*	*	*	*		*	*	*	*	*	*				
REMBISZEWSKI (1971)	*	*									*	*		*	*	*
O'GORMAN (1974)				*								*				
FOLZ & NORDEN (1977)	*	*		*	*		*	*				*				
NILSSON (1979)	*	*		*	*											

* O'Gorman's study was concerned with predation by smelt on Alewives. He indluded references to Mysis relicta in the diet since many stomachs "were gorged" with the organisms. Other less dominant organisms were not included in the list of organisms consumed.

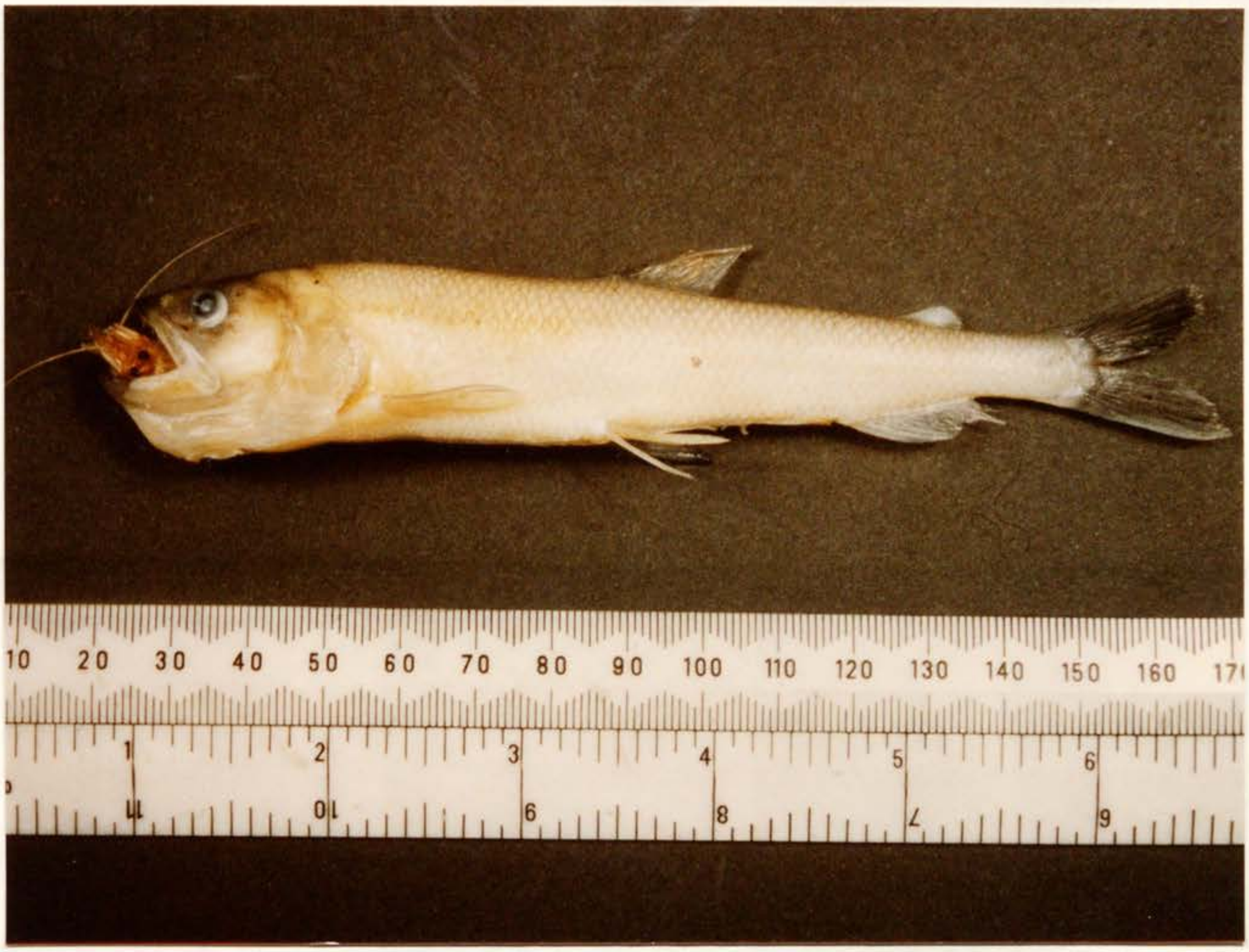
TABLE 69: The composition of the diet of several populations of landlocked smelt, Osmerus spp.

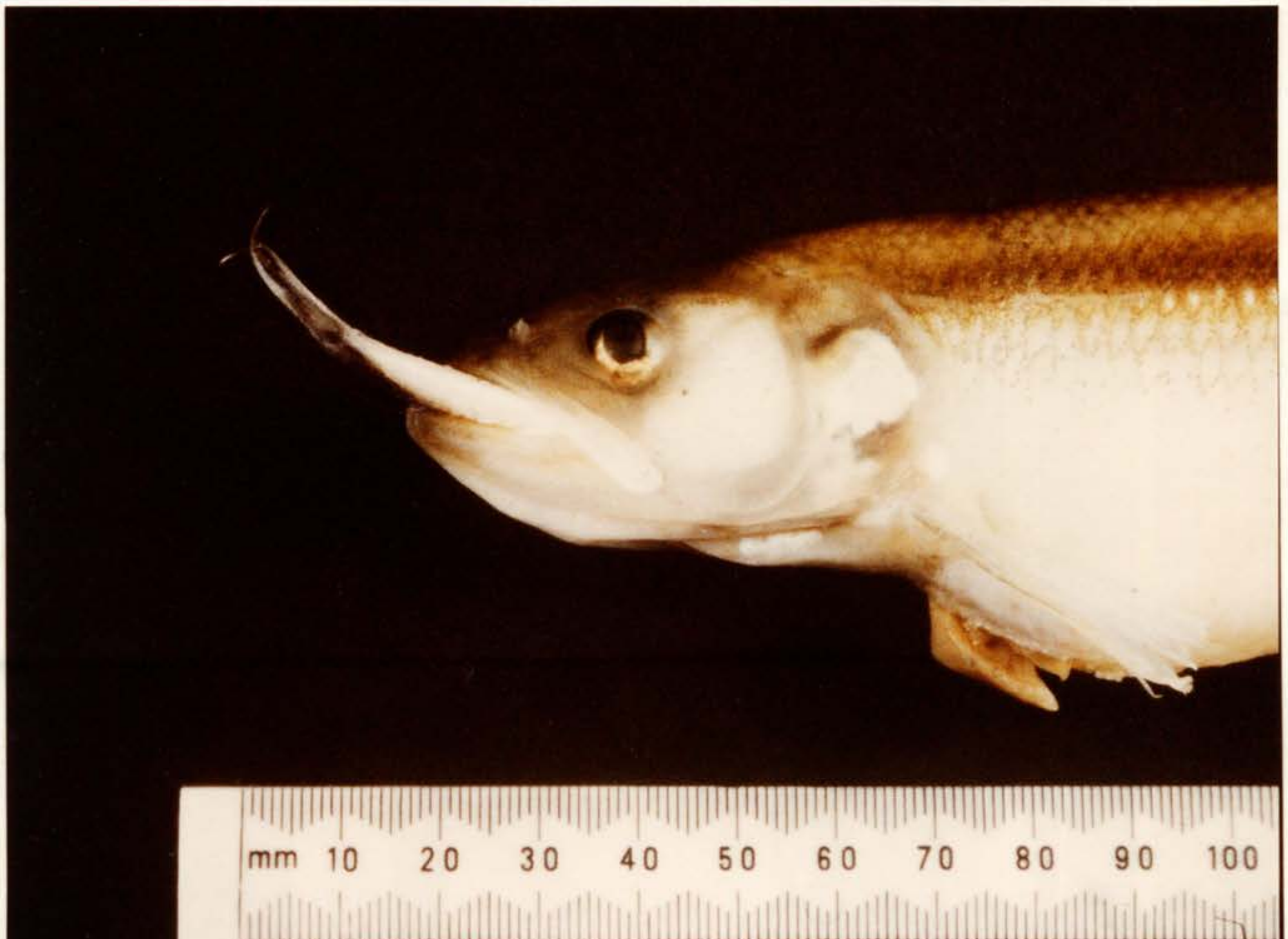
While planktonic crustaceans, amphipods, mysids and other fish species are common to the diet of both estuarine and freshwater populations, the diet of landlocked smelt also includes various forms of insect.

Greene (1930), Gordon (1961) and Rembiszewski (1970) found evidence of an algal component in the diet of landlocked smelt and Rembiszewski (1970) concluded that smelt were 'omnivorous'. However, since Rembiszewski (1970) considered that smelt could dig their food out of the substrate, the possibility that the algal remains were ingested accidentally, as suggested for winter flounder, Pseudopleuronectes americanas, by Wells, Steele and Tyler (1973), cannot be excluded.

The results from both the river Thames and the river Cree indicate that the relative importance of small food organisms such as mysids and Eurytemora affinis decreases with increasing fish size while the relative importance of larger food organisms such as other fish species and Crangon crangon increases in the larger size groups. Predation by the larger size groups of smelt, Osmerus spp., on larger food organisms such as shrimps, other large crustaceans and fish has been reported by Nordquist (1910), Gordon (1961), Belyanina (1969), Burbidge (1969) and Anderson and Smith (1971).

Increased piscivority with increasing fish size is well known amongst predatory fish (Price, 1963) and the smelt from the rivers Thames and Cree are no exception. Although Jensen (1949), Gordon (1961), Price (1963), Belyanina (1969), Burbidge (1969), Anderson and Smith (1971), O'Gorman (1974), Foltz and Norden (1977a) and Selgeby, MacCallum and Swedberg (1978) all made reference to increasing





PLATES 13 & 14: Examples of the diet of smelt.

Top: A male 1+ years old smelt from the river Thames which had ingested a brown shrimp prior to capture at CEGB West Thurrock.

Bottom: A female 2+ years old smelt from the river Cree which had ingested an underyearling smelt prior to capture in the gill net.

piscivority with increasing size, the size at which smelt first adopt a piscivorous component in the diet appears to be variable. Thus, the lower size limit for piscivority in smelt, Osmerus mordax, has been reported as 125 mm (Anderson and Smith, 1971) and 143 mm (O'Gorman, 1974). Selgeby, MacCallum and Swedberg (1978) showed that the proportion of smelt, Osmerus mordax, that contained lake herring, Coregonus artedii, larvae increased from 0% at lengths of 40 - 49 mm, to 70 - 100% at lengths of 100 - 190 mm. Foltz and Norden (1977a) found that smelt, Osmerus mordax, greater than 180 mm consumed three times more fish than smelt less than 180 mm and Price (1963) found that smelt, Osmerus mordax, greater than 126 mm consumed more fish than smaller specimens.

Piscivority occurred in all the size groups investigated in this study but reached a peak in the 200 - 299 mm size class from the river Cree. The smallest smelt that included another fish in its diet was 72 mm long.

In view of the tendency for larger smelt to adopt a piscivorous diet, considerable attention has been paid to possible interactions between smelt and other species of fish. In the Great Lakes, the smelt, Osmerus mordax, was accused of being a major contributor to the decline of the native fisheries. Predation by smelt was believed to have been the major cause of the destruction of trout stocks in Lakes Michigan and Huron (Gordon, 1961) and of the severe decrease of lake trout (Gordon, 1961) and lake herring (Anderson and Smith, 1971) in Lake Superior. Kendall (1927) however, believed that "under no conditions are they [smelt] a menace to young trout or salmon" and Schneberger (1936) supported this statement by showing that smelt and lake trout fry would be separated by their respective depth distributions. Selgeby, MacCallum and Swedberg (1978) concluded that while smelt consumed lake herring larvae, the predation was not a major factor suppressing the lake herring populations. However, while size selective fishing and lamprey predation have now been identified as the major factors reducing the spawning stocks in the Great Lakes, the effect of the planktivorous phase of the life-cycle of fishes such as alewives, Alosa pseudoharengus, and smelt, Osmerus mordax, on a reduced number of pelagic eggs may have inhibited recruitment and thus contributed to the decline of those species with pelagic eggs (Crowder, 1980).

Cannibalism has been reported from a large number of smelt, Osmerus spp., populations (HMSO, 1892; Smitt, 1895; Kendall, 1927; Creaser, 1928; Greene, 1930; Schneberger, 1936; Beckman, 1942; Jensen, 1949; Van Oosten, 1953; Pirojnikov, 1955; Gordon, 1961; Amstislavsky and Brussynina, 1963; Abdel-Malek, 1966; Rembiszewski, 1970; Anderson and Smith, 1971; O'Gorman, 1974) and the results of this study show that in the river Cree underyearling smelt was the single most important food organism to be consumed.

Nikolsky (1963) believed that the transition to feeding on their own young in years of peak year classes enabled the smelt, Osmerus eperlanus, to effect regulation of abundance and thereby reduce the aggravation of feeding relationships which might arise as a result of over-population. However, in view of the low diversity and low abundance of other species of fish in the gill net catches from the river Cree (see Table 6) it seems possible that feeding on their own young may enable adult smelt to maintain high growth rates in an environment containing few other fish, as reported for perch, Perca flavescens, by Nikolsky (1963). In the river Thames at

West Thurrock, where some 75 other species of fish have been recorded (Andrews *et al*, 1982) and the abundance level of smelt is such that in 1978 a peak count of 2,500 smelt was recorded in a single sampling period (Andrews *et al*, 1982), no cannibalism was recorded.

Belyanina (1969) has reported that the young of all smelt populations feed on zooplankton and Burbidge (1969) considered that the food of juvenile smelt, *Osmerus mordax*, in both the marine and freshwater environments consisted of small crustaceans. Entomostraca were found to be the dominant food organisms of 0-group smelt by Nordquist (1910), Gordon (1961) and Anderson and Smith (1971). The results of this study showed that *Eurytemora affinis* contributed numerically to the diets of the 50 - 99 mm and 100 - 149 mm size classes from the Thames, and to the diet of the smaller size class from the river Cree. However, its contribution to the diet in terms of frequency of occurrence, volume and IRI was very small. It is possible that zooplankton contributed to the diet of smelt at a size prior to their occurrence in the screen and gill net samples. However, by the time smelt were large enough to appear in the samples, mysids in the case of 0-group Thames fish and mysids and small crangons in the case of 0-group Cree fish dominated the diets. Analysis of the stomach contents of 0-group Cree smelt in the size range 37 - 42 mm (n = 4) which had been consumed by adult smelt in the summer sample also revealed *Neomysis integer* as the only food organism. It would therefore appear that apart from an occasional occurrence in the diet of larger specimens, copepods, if consumed, would serve as 'first food' and that at an early age mysids become the major dietary component.

It has been shown in Section 6:3:3 that in the river Thames

DATE	GAMMARIDS	MYSIDS	DOMINANT FOOD ITEM (%F)
9. 2.81	**	***	MYSIDS
24. 2.81	*	**	
10. 3.81	**	**	MYSIDS
7. 4.81	***		GAMMARIDS
22. 4.81			
22. 5.81	**		
4. 6.81	**		
10. 6.81	***		GAMMARIDS
19. 6.81	***		
2. 7.81	***	**	GAMMARIDS
21. 7.81	**	**	
3. 8.81	***	**	MYSIDS
18. 8.81	***	**	
1. 9.81	**	**	MYSIDS
16. 9.81	***	**	
2.10.81	**	**	MYSIDS
15.10.81		**	
2.11.81	**	**	MYSIDS
16.11.81	*	**	
1.12.81	*	**	
15.12.81		**	MYSIDS
30.12.81	**	**	
13. 1.82	**	**	
28. 1.82	**	**	MYSIDS
11. 2.82	**	*	GAMMARIDS
26. 2.82	**		
12. 3.82	**		GAMMARIDS
29. 3.82	***		
13. 4.82	***		GAMMARIDS
26. 4.82	**		
10. 5.82	***		GAMMARIDS
25. 5.82	***	*	

TABLE 70: The abundance of mysids and gammarids on the screens at CEGB West Thurrock, and the dominant food item in the diet of smelt as indicated by frequency of occurrence data (data regarding screen catches supplied by Thames Water Authority). * few; ** several; *** many.

mysids and gammarids exhibit marked seasonality in the diet of smelt. Table 70 indicates the abundance of both of these organisms on the screens at CEGB West Thurrock and the dominant organism in the diet of smelt (as indicated by frequency of occurrence) for the corresponding month. The large aperture of the screens (9.5 mm square) relative to the size of the organisms would result in only a small proportion of these organisms being retained, but if it is assumed that a constant proportion of those entering the system are retained then the data can be used to indicate relative abundance.

Table 70 shows that gammarids were recorded on the screens throughout the year whereas mysids were absent from the screen catch during April, May and June 1981, and February - May 1982. During these periods gammarids dominated in the diet of smelt whereas during the periods when mysids were present in the screen catches they dominated the diet.

Mysids are known to form aggregations of various kinds and to undergo tidal and seasonal horizontal migrations (Makings, 1977). If Neomysis integer undergoes such a tidal horizontal migration it may support the theory of tidally synchronised feeding in smelt. Furthermore, Mauchline (1971a) showed that Neomysis integer commences breeding in February with intensive breeding occurring in April and May. At such times, Neomysis integer forms shoals and swarms (Mauchline, 1971b). The absence of Neomysis integer from both the screen catch and the diet of smelt may be a result of breeding aggregations and/or a seasonal breeding migration. Moore and Moore (1976b) also found Neomysis integer to be scarce in the reservoir of Oldbury power station during April-May and also between August - September.

In the absence of mysids, smelt in the Thames adopt a predominantly gammarid diet but they recommence feeding on mysids when they again become available. They would therefore appear to exhibit a marked preference for mysids as also reported by Pirojnikov (1955), Foltz and Norden (1977b) and Sedgwick (1979). Moore and Moore (1976a, 1976b) showed that Neomysis integer was relatively immobile and therefore unable to escape predation and, unlike Gammarus salinus, was never concealed among weeds and debris. Ware (1972) considered that prey exposure was likely to play a major role in prey selection, particularly where the predators were obligate visual hunters and Johannes and Larkin (1961) found that rainbow trout, Salmo gairdneri, only attacked Gammarus spp. that appeared at the periphery of the weed bed. The absence of Praunus flexuosus from the diet of both Thames and Cree smelt may also be a result of their association with weeds and their tendency to be spatially dispersed rather than shoaling. Furthermore, unlike the euryhaline Neomysis integer, Praunus flexuosus prefers higher salinities and therefore undergoes restricted tidal migrations (Mauchline, personal communication).

In view of the preference for mysids, it is somewhat surprising to find that the periods of peak feeding activity, as reflected by the mean fullness index, correspond to the periods when gammarids are dominant in the diet. However, it should be noted that the fullness index is a measure of bulk and not nutritional value. The results of Moore and Moore (1976a, 1976b) would suggest a greater expenditure of energy in exploiting gammarids as prey. Furthermore, the digestibility of gammarids appears to be less than that of mysids since the remains of gammarids were still clearly recognisable in the lower gut following gastric digestion, while the only evidence of mysids was undigested eyes.

Crangon crangon, also exhibited a seasonal pattern of occurrence in the diet of Thames smelt, being consumed from July - December 1981 and in February 1981 and 1982. Meyer-Waarden & Tiews (1957) showed that brown shrimp undergo an upstream feeding migration in summer in response to elevated summer temperatures and in autumn, the shrimps migrate downstream again to the warmer waters offshore (Boddeke, 1976). Until 1981, upstream migration of *Crangon crangon* in the Thames took place in the autumn, which Sedgwick (1979) attributed to artificially elevated temperatures in the middle reaches. In 1981 however, this autumnal influx did not occur and numbers were relatively constant throughout the year at West Thurrock (Andrews *et al*, 1982). The overall importance of *Crangon crangon* to the diet of Thames smelt was relatively low despite this availability throughout the year. Moore and Moore (1976a) attributed the low exploitation of this species by flounders, *Platichthys flesus*, to a combination of a size selection and the prey's ability to escape, particularly in turbid conditions. Moore and Moore (1976b) showed that the eel, *Anguilla anguilla*, could exploit *Crangon crangon* more successfully than the flounder because it approached the prey slowly and did not invoke the "escape reaction". Smelt fishermen are familiar with the fact that smelt approach their bait slowly, stop and suck the bait in (Bigelow and Schroeder, 1953), and these authors concluded that it is a mystery how smelt succeed in capturing animals as active as shrimps while adopting this mode of feeding. However, the results of Moore and Moore (1976b) show that this approach is necessary in order to avoid stimulating the escape reaction which in turbid conditions invariably results in the prey escaping. It therefore seems unlikely that the low utilisation of *Crangon crangon* by Thames smelt is a result of a low capture efficiency, but rather is a size related morphological limitation.

In the river Cree, the most obvious seasonal trend was that of the occurrence of underyearling smelt in the diet. Smelt of the 1981 year class (size range 76 - 97 mm) dominated the diet of adult smelt in the autumn sample but were completely absent from the winter sample and only one was consumed in the spring sample. By the time the summer samples were collected cannibalism was again present with adults consuming underyearling fish of the 1982 year class (size range 37 - 42 mm).

Burbidge (1969) found that adult smelt only fed on underyearling smelt in August and that segregation in the water column during summer and the large size of underyearling smelt after August limited the opportunities for cannibalism. Ferguson (1965) also reported segregation during the period of stratification and considered that by the time mixing of the water column occurred underyearling smelt were too large to be consumed.

A similar phenomenon may have been operative in the Cree with the majority of underyearling fish being too large to be consumed after autumn. The underyearling smelt consumed in autumn were of smaller lengths (78 - 97 mm) than those 0-group smelt taken in the gill net (mean length 105 mm). However, it is not possible to isolate whether the size selectivity was due to the adult smelt utilising smaller than average fish or the gill net selecting for larger than average fish.

Rembiszewski (1970) found that adult smelt selected underyearling smelt of approximately 50 mm length, although on one occasion an adult of 178 mm was found to have consumed a smelt of 106 mm.

While size selection may have been responsible for the absence of underyearling smelt from the diet of adults during winter and spring, other factors may have been responsible eg. segregation of age groups prior to spawning or decreased metabolic demands during winter.

SUGGESTIONS FOR FUTURE RESEARCH

It was stated in the introduction to this thesis that the objectives of this study were to provide baseline ecological data for the smelt in Britain and to stimulate interest in, and provide pointers for future research on, a species which has hitherto been scientifically ignored by British ichthyologists. The nature of the study was such that many possible avenues for further research were identified but left 'unexplored' because of time and financial restrictions.

The role of the odouriferous substance in the biology of smelt, and other species of fish, is at the moment conjectural and Berra et al, (1982) considered that further studies should be carried out to test the hypothesis that the chemicals involved are alarm substances. Identification of these substances may also be of phylogenetic significance.

The occurrence of hermaphroditic smelt in the river Thames, and in other populations of smelt, is also of great interest and further studies involving large scale histological work should be conducted in an attempt to clarify the adaptive significance of the condition.

Transfer studies were not possible within the timespan of this research but controlled introductions would have been useful in determining the relative contribution of genetic and environmental factors to the 'stunted' growth of Thames smelt. Attempts to re-introduce smelt to those rivers where the species has suffered a decline may also be useful and provide a valuable by-catch in the face of declining salmon stocks. Maitland (1979) believed that attention should be given to introducing smelt to freshwater using local anadromous stocks. In view of their considerable value as a forage base in North American waters, introductions of smelt may be of value in managed trout fisheries.

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APPENDICES

APPENDIX 1: LIST OF PERSONAL COMMUNICATIONS

Mr M.J. Andrews, Metropolitan Pollution Control, Thames Water Authority, Mogden

Mr G.S. Armstrong, Thames Water Authority, Reading.

Berwick Salmon Fisheries Company, Berwick-upon-Tweed.

Mr D.J. Bremner, (Salmon fisherman), The Shore, Alloa.

Mr M. Bulleid, Thames Water Authority, Reading.

Mr Clarke, Fisheries Office, Pittenweem.

Dr. D. Cragg-Hine, North-West Water Authority, Warrington.

Dr. R.C. Cresswell, Yorkshire Water Authority, Leeds.

Dr. P. Dando, Marine Biological Association of the UK, Plymouth.

Mr C. Durie, North-West Water Authority, Lancaster.

Dr. M. Elliott, Forth River Purification Board, (Estuaries), Edinburgh.

Mr D. Evans, Lancashire & Western Sea Fisheries Joint Committee, Lancaster.

Mr H. Gardiner, (Salmon netsman), 128 Morecambe Road, Lancaster.

Mr Gray, Deveron District Salmon Fishery Board.

Mr Grey, Ayr Wholesale Fish Merchants Association, Ayr.

Mr A. Harrison, (Angler on Welton Ponds), Pontefract, Yorkshire.

Mr A.V. Holden, Department of Agriculture and Fisheries for Scotland, Pitlochry

Mr B.E. Jones, Welsh Water Authority, Caernarfon.

Mr B. Joslin, Southern Water Authority, Maidstone.

Dr. R.S.J. Linfield, Anglian Water Authority, Huntingdon.

Dr. P. Maitland, Institute of Terrestrial Ecology, Edinburgh.

Dr. J. Mauchline, Scottish Marine Biological Association, Oban.

Dr. D.E. McAllister, National Museum of Natural Sciences, Ottowa, Canada.

Dr. D.H. Mills, Department of Forestry & Natural Resources, Edinburgh University

Dr. C. Moriarty, Department of Fisheries & Forestry, Abbotstown, Co. Dublin.

Mr H.G. Pearce, Freshwater Fisheries Unit, Liverpool University.

Dr. E.J. Perkins, University of Strathclyde, Kilcregan.

Dr. R. Sedgwick, Severn-Trent Water Authority, Nottingham.

Dr. D. Solomon, Ministry of Agriculture Fisheries and Food, Lowestoft.

Mr W.J. Walker, Northumbrian Water Authority, Gosforth.

Ms L. Wilson, Stinchar/Girvan District Salmon Fishery Board, Girvan.

Dr. J.S. Wortley, Anglian Water Authority, Huntingdom.

Dr. A. Wheeler, British Museum (Natural History), London.

The following also provided information regarding the distribution of smelt in Britain:

Central Electricity Generating Board.

Central Fisheries Board of Ireland.

Department of Agriculture & Fisheries for Scotland.

Department of Agriculture for Northern Ireland.

Fishmonger's Company.

Fleetwood Fish Merchants Association.

Freshwater Biological Association.

Hull Fish Merchants Association.

Irish Sea Fisheries Board.

London Fish Merchants Association.

Manchester Wholesale Fish Merchant's Association Limited.

Ministry of Agriculture, Fisheries & Food.

Nature Conservancy Council.

University College Galway.

YEAR	DATE OF ENTRY INTO RIVER	MEAN DAILY TIDE HEIGHT (m)
1926	9th March	8.4
1927	2nd March	6.7
1928	4th March	8.0
1929	1st March	7.9
1939	5th March	8.4
1931	7th March	9.5
1936	2nd March	6.7
1937	4th March	7.3
1938	4th March	8.8
1939	1st March	7.0
1943	2nd March	7.3
1945	8th March	6.5
1946	16th March	8.4
1949	3rd March	8.2
1961	21st March	8.4
1964	12th March	8.2
1980	10th March	7.5
1981	10th March	9.5

APPENDIX 2: Date of entry of smelt into the river Cree in relation to tide height over the period 1926 - 1981.
(Source: R. Plunkett, Salmon netsman).

PARTICLE SIZE CLASS	PERCENTAGE OF TOTAL WEIGHT OF SAMPLE IN EACH SIZE CLASS													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
>63.5mm	17.3	6.8	4.3	-	61.4	38.7	42.9	70.5	11.7	34.6	68.2	58.6	23.1	37.8
25.4mm-63.5mm	36.2	58.3	38.4	-	24.3	46.5	35.3	11.1	71.3	31.6	16.7	21.2	36.7	14.4
9.5mm-25.4mm	21.5	19.1	38.8	-	9.5	7.7	8.8	11.6	13.2	13.6	5.7	7.7	23.6	30.1
2.0mm-9.5mm	16.4	12.6	18.7	72.9	4.5	6.6	11.9	6.4	2.6	18.4	8.0	10.4	16.4	17.6
1.4mm-2.0mm	0.6	1.2	2.2	0.3	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
850µm-1.4mm	6.9	1.3	1.4	22.4	<0.1	0.2	0.4	0.2	0.3	0.7	0.6	1.1	<0.1	<0.1
250µm-850µm	1.0	0.6	1.2	4.3	<0.1	0.2	0.5	0.2	0.8	0.8	0.7	0.8	<0.1	<0.1
<250µm	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1

Samples 1 - 4 from the east bank
Samples 5 - 14 from the Newton Stewart town bank

APPENDIX 3: Analysis of the spawning substrate from the river Cree.

Samples were collected along transects situated in areas of spawning activity which had been exposed by receding water levels. The substrate was collected from ½ m quadrants to a depth of 100 mm and transported in fertilizer sacks to the laboratory. The samples were passed through a stack of sieves, the mesh sizes of which are given above and the resultant fractions were dried at 100°C for 1 day and weighed (± 0.1 g).

MONTH	NO. FISH INFECTED	% INCIDENCE	TOTAL NO. PARASITES	MEAN NO. INFECTED FISH	MAXIMUM
FEBRUARY	5	25.0	17	3.4	10
MARCH	7	38.9	30	4.3	13
APRIL	3	16.7	6	2	3
MAY	*	*	*	*	*
JUNE	*	*	*	*	*
JULY	2	40.0*1	3	1.5	2
AUGUST	0	0	0	0	0
SEPTEMBER	2	11.8	2	1	1
OCTOBER	1	4.5	3	3	3
NOVEMBER	4	13.3	5	1.2	2
DECEMBER	5	11.1	5	1	1
JANUARY	5	16.1	9	1.8	3
FEBRUARY	4	16.0	11	2.7	6
MARCH	6	13.6	44	7.3	18
APRIL	5	8.3	11	2.2	5
MAY	2	5.0	2	1	1

* no samples.

*1 based on the analysis of only 5 digestive tracts.

The incidence and degree of infection of Thames smelt with the nematode *Thynnascaris adunca*.

SEASON	NO. FISH INFECTED	% INCIDENCE	TOTAL NO. PARASITES	MEAN NO. INFECTED FISH	MAXIMUM
AUTUMN	5	7.8	9	1.8	4
WINTER	11	15.5	29	2.6	13
SPRING	13	15.1	103	7.9	32
SUMMER	4	8.5	15	3.7	6

The incidence and degree of infection of Cree smelt with the nematode *Thynnascaris adunca*.

APPENDIX 4: The incidence of parasites in the digestive tracts of smelt from both study sites.

Thynnascaris adunca is a very common parasite of marine fish in British waters. Fish acquire the parasite by feeding on the intermediate hosts which include copepods and mysids.

APPENDIX 5: PUBLICATIONS.

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A note recording the occurrence of hermaphroditic smelt, *Osmerus eperlanus* (L.) from the river Thames, England

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Of a sample of 703 smelt, *Osmerus eperlanus*, from the estuary of the river Thames, 2·6% were identified as being synchronous hermaphrodites. The fish are compared with previously reported hermaphroditic smelt.

I. INTRODUCTION

Hermaphroditism has been reported more frequently in bony fishes than in any other group of vertebrates except the cyclostomes. However, with the exception of those species in which the condition is normally present, hermaphroditic individuals are rare (Atz, 1964).

Recorded hermaphroditism in Salmoniformes is very rare and the majority of the data are concerned with reporting the condition in single specimens of a given species. Thus hermaphroditic trout, *Salmo fario* (Stewart, 1891); king salmon, *Oncorhynchus tshawytscha* (Rutter, 1902); trout (De Beer, 1924); silver salmon, *Oncorhynchus kisutch* (Crawford, 1927); cut-throat trout, *Salmo clarkii* (Turner, 1946); steelhead trout, *Salmo gairdneri* (Gibbs, 1956); chum salmon, *Oncorhynchus keta* (Uzmann & Hesselhont, 1958); rainbow trout, *Salmo gairdneri* (Ross, Yasutake & White, 1963); lake whitefish, *Coregonus clupeaformis* (Chen, 1969); and powan, *Coregonus lavaretus* (Scott, 1975) have all been recorded. With the exception of Rutter (1902), who observed the condition in two king salmon, all of these reports dealt with the occurrence of individual hermaphrodites often observed during large-scale sampling operations.

Unparalleled among the Salmoniformes are Hofmeister's (1939) observations on the smelt, *Osmerus eperlanus*, population of the river Elbe where 3·7% of a sample of more than 1000 fish were identified as hermaphrodites. Externally these fish appeared to be normal males, possessing the nuptial tubercles or pearl organs which are a male secondary sexual character in this species. Internally, the ovotestis was predominantly testicular but ovarian tissue was also present and ripe ova were occasionally present in the sperm ducts. Internal, self-fertilization was therefore a physiological possibility. The condition has since been reported by Lillelund (1961) who identified 2% of smelt samples from the river Elbe as being hermaphroditic. With the exception of an isolated specimen recorded by Jensen (1949) no other record of hermaphroditism in the smelt exists in the literature.

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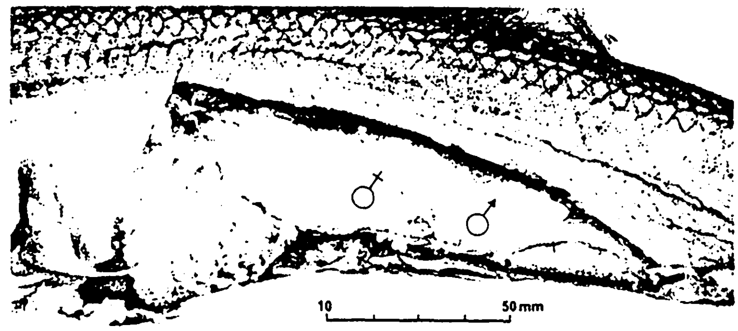

FIG. 1. The gross morphology of the ovotestis of a mature 1+years old smelt, *O. eperlanus*. The testicular component is located in an uncharacteristically posterior position.

II. MATERIALS AND METHODS

The hermaphroditic individuals were identified from monthly samples (Feb. 1981–Mar. 1982) of smelt collected from the screens of CEGB West Thurrock power station. (Huddart, 1971). The fish were fixed in a 4% aqueous solution of formaldehyde and examined in the laboratory.

Tissues for light microscope evaluation were dehydrated in a graded series of ethanol, embedded in paraffin wax and sectioned on a rotary microtome. Tissue sections cut at 10 µm were mounted on glass slides and stained with haematoxylin and eosin.

III. RESULTS AND DISCUSSION

Eighteen individuals (2·6%) of a total sample of 703 fish were identified as hermaphrodites. Externally, the fish resembled mature females and internal examination revealed that the ovotestes were predominantly ovarian (Fig. 1). In addition the ovotestes contained small areas of testicular tissue which were generally located in the anterior region of the gonad. The histological appearance of the ovotestes is shown in Fig. 2. In four (22%) of the hermaphroditic individuals, only the larger left gonad was ovotesticular with the right gonad being entirely ovarian while in the remaining specimens (78%) both the right and left gonads were ovotesticular.

In line with the findings of Hofmeister (1939), who found that the condition was prevalent amongst mature 2-year-old fish, the majority (78%) of the Thames hermaphrodites belonged to the 1979 year class. One (5·5%) hermaphroditic individual came from each of the 1978 and 1980 year classes and two (11%) came from the 1981 year class. In contrast, Lillelund (1961) found that the O-group fish contained the highest incidence of hermaphroditism but concluded that many of these individuals would become normal males later.

The condition has not been recorded from a sample of over 700 smelt from the river Cree in Galloway or from samples from the river Lune, Lancashire, examined by the author. Atz (1964) concluded that since hermaphroditic ruffe, *Gymnocephalus cernua*, had also been recorded from the river Elbe, the condition must be attributable to environmental conditions prevailing in that river.

On the basis of the results from the river Thames, it would appear that given certain environmental conditions the normally gonochoristic smelt develops teratological hermaphroditism at a detectable level within the population.

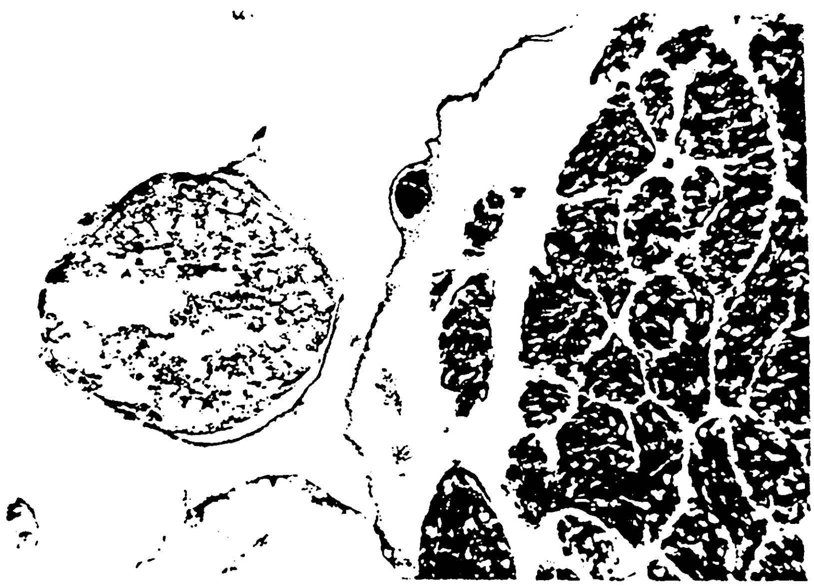

FIG. 2. The histological appearance of the ovotestis showing a mature oocyte (diameter 1 mm) and seminiferous tissue.

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